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CHAPTER

Numerical and Mathematical Abilities in Children: Behavioral and Neural Correlates

Teresa Luculano, Roi Cohen Kadosh

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Abstract

This chapter reviews the cognitive and neural mechanisms for numerical and mathematical development. It provides converging evidence that from a rudimentary, non-symbolic “number sense” representation that is assumed to exist even in non-human species, the human mind develops its unique symbolic representational system to accurately represent and manipulate numerical quantities. This process is non-trivial, it is slow, and it requires the *push-and-pull* of multiple neurocognitive systems. These include: (i) those supporting visual and verbal perception/decoding in the occipital and temporal cortices, (ii) regions of the frontal eye-fields and the posterior parietal cortex involved in active manipulation and updating processes, (iii) memory association processes within the medial temporal lobe, and (iv) executive control processes anchored in the frontal cortices. The present chapter proposes a neurocognitive model whereas the successful acquisition of our modern symbolic code for mathematics is gradually refined through the dynamic interaction of these neurocognitive systems throughout development. Depending on the specific cognitive weaknesses of the individual, training, intervention, and educational approaches should hence be designed to comprehensively “stimulate” part or all these neurocognitive systems to achieve the most optimal learning outcomes.

Keywords: [mathematical development](#), [numerical development](#), [number sense](#), [arithmetic](#), [quantity](#), [memory](#), [learning](#), [intervention](#), [brain stimulation](#)

Subject: [Developmental Psychology](#), [Psychology](#)

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Introduction

The ability to compare and reason about numerical attributes of sets develops very early in life. Infants and even newborns are able to perceptually discriminate which of two sets is larger in numerosity for 1:3 ratios (Izard et al. 2009), with a steep developmental curve in acuity within the first year of life (i.e., by nine to ten months they are able to “solve for” 2:3 ratios) (Lipton and Spelke 2003; Xu and Arriaga 2007). This ability seems to be present also in several mammalian and non-mammalian species (Agrillo et al. 2008; Brannon and Terrace 2000; Dacke and Srinivasan 2008; Ditz and Nieder 2015; Meck and Church 1983; Nieder et al. 2002; Shumaker et al. 2001; Tudusciuc and Nieder 2007) and has been referred to as the “number sense”. Inasmuch as rudimentary numerical skills such as these are ontogenetically and phylogenetically ancient, the ability to reason symbolically about these attributes, which is the essence of modern mathematics, is an extremely recent acquisition in our lineage and requires the coordinated support of several brain systems over development.

When a child first learns mathematical symbols such as 1, 2, 3, and 4, these are usually associated with meaningless counting sequences (Sarnecka and Carey 2008). Only later, and with more formal teaching, these symbols are associated with their corresponding semantic numerical meanings and their intrinsic properties (Gelman and Gallistel 1978; Sarnecka 2015). These include simple rules of cardinality and ordinality that precede, and are foundational, to the ability to reason about symbolic numerosities and eventually being able to perform formal arithmetical operations on them (i.e., to add, to subtract, etc.). Cardinality includes all principles derived from bijective and injective functions such as: (i) when the elements of one set can be put in one-to-one correspondence with the elements of the other, then the two sets have the same numerosity (i.e., they are exactly equal)—bijection; and (ii) the set denoted by the greater number includes the set denoted by the smaller one (e.g., a set of four items will include a set of three items)—injection. This means that adding (or subtracting) an item to (from) a set, will affect its numerosity.

Formal principles of ordinality emerge from cardinal principles: the final number of a counting sequence represents the cardinality of that sequence; and the next word of the counting sequence can be obtained by adding one unit to the current cardinality (Giaquinto 1995; see also Gelman and Gallistel 1978). As previously mentioned, the approximate, non-symbolic equivalent of these types of abilities is present already in infants (for a review, see de Hevia 2016). Habituation type of paradigms have shown that infants as young as four to six months are able to succeed—with adequate accuracy levels—on tasks that require to compare, add, or subtract non-symbolic numerosities from sets: they are aware when changes in numerosities occur (McCrink and Wynn 2007), and they seem to have an accurate arithmetic expectancy regarding numerical transformations on them (Wynn 1992, 1998). Some rudimentary ordinality properties also seem to emerge very early during development. A recent study has shown that preverbal infants as young as four-months old can detect ordinal relationships of size-based and numerical-based sequences (de Hevia, Addabbo, et al. 2017; see also Brannon 2002).

Yet, within our exact (and symbolic) number system, both these cardinality and ordinality properties are highly complex to acquire, require many hours of formal education and are susceptible to many heuristic-based and confusion errors (Gelman and Gallistel 1978; Houdé and Tzourio-Mazoyer 2003). The question is, how—during their first years of schooling—most children become efficient “symbolic calculators”? How do they successfully step away from wrong counting procedures, inaccurate applications of one-to-one principles, to finally (and successfully) learn arithmetic rules and procedures on Arabic numerals?

The recent advent of several non-invasive, in vivo neuroimaging techniques, such as electroencephalography (EEG) and functional magnetic resonance imaging (fMRI), has started to shed light into how the brain supports this knowledge acquisition such that, at some point during development, a

child “just knows” that $3 + 4 = 7$. These functional brain systems include visual and auditory association cortices—and their interactions. These brain regions decode the visual and phonological features of the stimuli (i.e., the symbol “3” or the spoken word “three”), and have their hubs in the higher level visual cortex, particularly in and around the fusiform gyrus (FG) (Abboud et al. 2015; Ansari 2008; Cantlon et al. 2006, 2009; Cantlon et al. 2011; Grotheer et al. 2016; Holloway et al. 2013; Shum et al., 2013); and in phonological and language processing regions anchored in the superior temporal sulcus (STS) and adjacent middle temporal gyrus (MTG) (Thompson et al. 2004). A semantic meaning to these originally arbitrary visual and verbal symbols arises through interactions with quantity processing systems residing in the posterior aspect of the parietal lobe, particularly the intraparietal sulcus (IPS). Developing such association provides the most sophisticated form of numerical reasoning: two sets of “four apples” and “four ideas” denote the same quantity, and this “shared property” can be referred to by the symbol (or word) “4.” The IPS has been systematically implicated in studies of number processing, number representation, and number reasoning (Cantlon et al. 2009, 2011; Castaldi et al. 2016; Castelli et al. 2006; Cohen Kadosh et al. 2007, 2008, 2011; Cutini et al. 2014; Dehaene and Cohen 1995; Dehaene et al. 2003; Hyde et al. 2010; Piazza et al. 2004, 2007; Vogel et al. 2015), possibly due to its topological proximity to cortical regions implicated in other cognitive tasks from which the ability to count and manipulate numbers/quantities may derive from, phylogenetically. These include regions of the frontal eye fields and posterior and superior parietal cortices supporting selective spatial attention (Corbetta and Shulman 2002; Schaffelhofer and Scherberger 2016), fine motor and eye movements (i.e., visuomotor; visual saccades; Cohen Kadosh et al. 2011; Simon et al. 2002), visual short-term memory (Knops et al. 2014; Luck and Vogel 1997, 2013; Todd and Marois 2004), as well as space perception (i.e., right-left discrimination in space; Gold et al. 1995; Hirnstein et al. 2011; Mayer et al. 1999), finger representations (Krinzinger et al., 2011), and allocentric and egocentric space representations (di Pellegrino and Làdavas 2015; Liu et al. 2017; Zaehle et al. 2007). These studies, which have been based mostly on adult participants, have suggested that once a child learns to form a systematic pairing between the number “3” and the quantity of “three items,” they can start performing formal arithmetical operations.

Learning rules and principles (i.e., “+” and “-” signs; or formal bijection/injection properties of sets), while starting to inhibit intuitive (and wrong) heuristics that do not meet the formal rule(s) learned is supported by cognitive control inhibitory processes within the prefrontal cortex (Houdé and Tzourio-Mazoyer 2003; Hung et al. 2018; Supekar and Menon 2012). The prefrontal cortex is responsible for different types of cognitive learning (Chein and Schneider 2012). One of the key roles of this brain region is to support cognitive control processes, such as inhibition. In the case of numerical processing, this includes mastering the concept that irrelevant, incongruent perceptual properties of sets, such as size, density, or length, do not influence the numerosity of that set. Concomitantly, interactions between the prefrontal cortex and posterior parietal regions—that form the working memory executive network—help to maintain and dynamically update intermediate results and procedures to facilitate calculation processes (Halgren et al. 2002; Zago et al. 2008). Finally, the hippocampus, within the medial temporal lobe, and its functional interactions with cortical regions, predominantly in the dorsolateral prefrontal and posterior parietal cortices, is involved in forming stable declarative memory associations (Davachi et al. 2003) between addends (i.e., “3” and “4”) and results (i.e., “7”), ultimately facilitating the automatic retrieval of arithmetical facts from memory (Qin et al. 2014; Rosenberg-Lee et al. 2018).

In this chapter our goal is to provide a comprehensive and timely overview on the aforementioned neurocognitive processes.

Numerical Abilities: Domain-Specific and Domain-General Cognitive Scaffolds

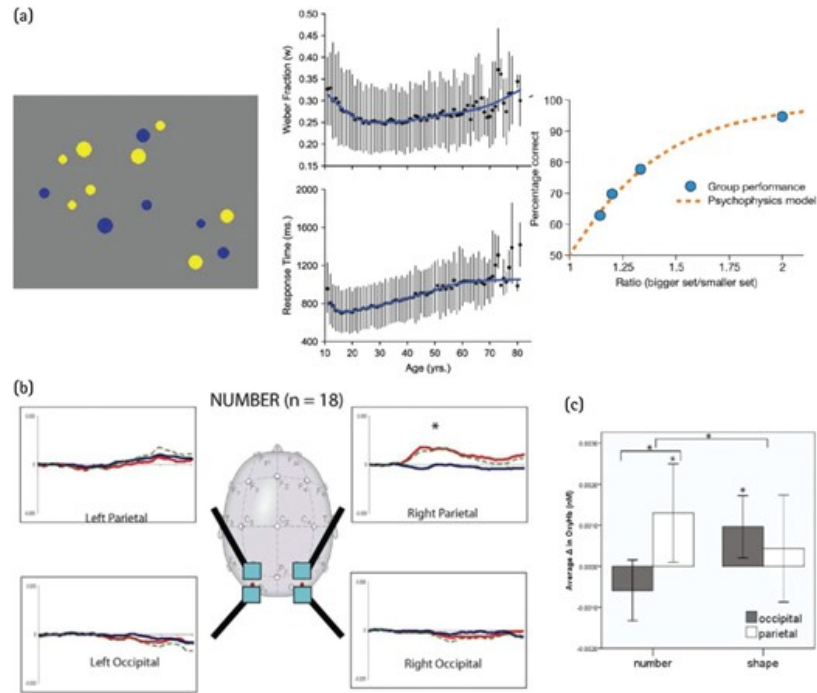
Developing Cardinal Skills

The numerosity of a set (i.e., its cardinality) is originally detected—yet processed approximately even for small numerosities—from a very early age (de Hevia 2016; Izard et al. 2009; Wynn 1992, 1998). Gradually, its acuity improves: within the first years of schooling, typically developing children can successfully discriminate sets of non-symbolic quantities with a 5:6 ratio (Halberda and Feigenson 2008). Such ability then steadily improves across development (Halberda et al. 2012) (Figure 1A), and it has been shown to be moderately associated with mathematical skills later in life (Halberda et al. 2008, 2012; see also Libertus et al. 2012) (Figure 1A). A stronger—and more reliable—domain-specific predictor of mathematical skills seems to be symbolic numerical magnitude processing (De Smedt et al. 2013; Schneider et al. 2017).

Critically, in a recent study, Vanbinst and colleagues report that the strength of the prediction of symbolic number comparison to arithmetical skills is comparable to that of phonological awareness to reading (Vanbinst et al. 2016; see also Gersten and Chard 1999).

The ability to discriminate between numerosities has been attributed to the appropriate functioning of the posterior aspect of the parietal lobes, particularly the IPS. Using near-infrared spectroscopy (NIRS) in a group of six-month olds, Hyde and colleagues demonstrated that the right IPS is sensitive to changes (1:2 ratio) of non-symbolic numerosities—but not shape—(Figure 1B,C); while right occipital areas are sensitive to changes in shape—but not numerosities (Hyde et al. 2010). A “cortical bias” of the posterior parietal cortex towards numerosity-specific aspects of the visual world has been demonstrated in infants as young as three months. Using EEG during a dishabituation paradigm, Izard and colleagues have shown that—similar to four-year-old children and adults—three-month-old infants’ electrical brain activity displays sensitivity to the cardinal properties of sets in regions of the posterior parietal lobe. Sensitivity to changes in other visual properties of the sets (i.e., object identity) was instead detected in regions of the occipital cortex—again, similar to four-year olds and adults (Izard et al. 2008).

Figure 1:



Development of cardinal skills—behavioral and neural correlates.

A. *Left*. Non-symbolic numerosity judgment task to assess numerical acuity—used with permission from Halberda et al. (2008).

Middle. Numerical acuity peaks at about the age of thirty years old—used with permission from Halberda et al. (2012). Two behavioral indices of numerical/numerosity proficiency are represented: on the *Top*: Weber-fraction. *Bottom*: Reaction times; *Right*: Numerical acuity significantly predicts mathematical skills later in life—used with permission from Halberda et al. (2008).

B. At six months of age, the right IPS is uniquely sensitive to changes in numerosity—used with permission from Hyde et al. (2010).

C. This effect is not evident for changes in shape (Hyde et al., 2010).

Note: Y-axes reflect relative change in oxygenated hemoglobin concentration (micromolars) measured by Near-Infrared Spectroscopy.

Notably, activity of the IPS has been shown to linearly scale with numerosities up to four or five (Xu and Chun 2006; i.e., the so-called “subitizing range”—or *visual short-term memory*—see Vogel and Machizawa 2004) which suggests the existence of an exact-tracking processing system for a small number of items, supported by the posterior parietal cortex (but see Piazza et al. 2002). Critically, subitizing skills are impaired in children with developmental dyscalculia (DD; a severe form of mathematical learning disability) (Koontz 1996; Landerl et al. 2004), and subitizing deficits have been associated with aberrancies in posterior parietal regions, particularly the IPS (Arp and Fagard 2005; Arp et al. 2006; Bruandet et al. 2004; Cipolotti et al. 1991; Paterson et al. 2006; Simon et al. 2005, 2008). More generally, it has been suggested/proposed that subitizing constitutes a fundamental building block for the appropriate development of arithmetical skills (Landerl et al. 2004; Reeve et al. 2012).

For numerosities >4 the acuity of the system decreases, and its pace of processing increases—even in typical populations (Chi and Klahr 1975). Yet, the cognitive processes associated with these (more difficult) numerosity discriminations are still supported, with increased specialization/modulation throughout development, by the IPS (Piazza et al. 2002). For instance, with larger numerosities (i.e., >4), a well reported finding is that the sensitivity to *distance/ratio* is reflected by faster and more accurate responses for larger *distance/ratio* (Moyer and Landauer 1967). Notably, at the brain level, the “neural distance/ratio effect” is marked by greater functional activity for numbers that are closer in numerosity (e.g., 4 versus 5). These are harder to discriminate compared to two numbers that are further apart from each other (e.g., 4 versus 9).

This effect has been observed in several brain regions, including the IPS in adults (Cohen Kadosh et al. 2011; Piazza et al. 2004). At younger ages, prefrontal cortex regions display a greater *neural distance/ratio effect* (Ansari and Dhital 2006; Price et al. 2007) for both symbolic and non-symbolic stimuli. Yet, other studies did show parietal modulation as a function of the “*distance/ratio effect*” already in children cohorts (Cantlon et al. 2006). We suggest that these mixed findings likely reflect the aid of working memory and executive processes to numerosity discriminations in children, and the greater degree of variability at younger ages—occurring before efficient numerical skills are consolidated. This suggestion fits well with the view that throughout development, the need of high-level (domain-general) processes for online tracking of items in space and their active storage and manipulation—heavily supported by dorsolateral prefrontal cortex regions and their connectivity with the parietal cortex—gradually becomes expendable when representations for approximate (and later exact) numerosities start to form within the IPS (i.e., anterior-to-posterior shift; see also later section “[Developing Formal Arithmetic](#)”).

Format-dependent symbolic representations (i.e., Arabic numerals) have also been shown to be modulated by the IPS (Vogel et al. 2017), as well as by high-level visual areas in the ventral temporal occipital cortex, particularly those adjacent to the FG (Grotheer et al. 2016). This brain region has been systematically reported to be highly sensitive to complex visual forms/stimuli (i.e., letters, faces, objects) (Gauthier et al. 1999, 2000). Interestingly, the FG seems also to subtend semantic representations of numbers: a *distance/ratio effect* has been reported in adults during numerical comparison tasks (Ansari 2008; Cantlon et al. 2009; Holloway et al. 2013; but see Cohen Kadosh et al. 2007). Such higher-order semantic specialization of the FG may be the result of the strengthening of the coupling within the dorsal visual stream that directly connects the visual and association cortices (Jung et al. 2017). Critically, the intrinsic functional connectivity between the FG and the IPS has been shown to significantly predict gains in mathematical abilities over development (Evans et al. 2015), suggesting a critical role of this pathway in children’s mathematical skill acquisition.

Together, this evidence suggests that both the IPS and the FG—and their functional and structural interactions—help to create neural representations of numbers in multiple formats (i.e., symbolic, non-symbolic). With the support of these two core brain systems, the human brain learns more complex mathematical computations through development and schooling, and with the support of other—less domain-specific—brain systems anchored in the prefrontal cortex and in the medial aspects of the temporal lobe.

Developing Ordinal Skills and Processing Spatio-Temporal Information

Most of the early work on numerical and mathematical cognitive skills has mainly focused on cardinality properties and their representations (Butterworth 1999, 2011; Dehaene et al. 2003; Piazza et al. 2006; Reeve et al. 2012), while ordinality aspects have largely been neglected.

Only quite recently, behavioral studies have begun to report a significant association between mathematical performance and semantic (i.e., magnitude-relevant) tasks of ordinality, such as: (i) ordinality judgements of triplets of symbolic numbers (Goffin and Ansari 2016; Kucian et al. 2011; Lyons et al. 2014); (ii) counting of forward and backward sequences/lists (O’Connor et al. 2018); as well as (iii) order working memory (WM) tasks (Attout et al. 2014; O’Connor et al. 2018). Critically, the ability to assess ordinal properties of numerical symbols seems to increase with development and schooling: in grades 1 to 2, performance on tasks tapping on cardinal properties of symbolic numbers has been shown to be the most predictive of arithmetical skills, while by grade 6, it is the performance on numerical ordinal tasks (with symbolic numbers) that emerges as the best predictor of arithmetic performance (Lyons et al. 2014; but see Attout et al. 2014).

Ordinality sequences—without a semantic magnitude connotation—are properties that emerge very early in life, when children start reciting counting sequences (i.e., number words) and even non-counting (i.e., alphabet, days of the week, months) lists (Gelman and Gallistel 1978; Sarnecka and Carey 2008). Ordering sequences without a semantic magnitude connotation (i.e., non-numerical ordering abilities) can also include remembering and processing spatio-temporal relationships such as daily events. Critically, a recent longitudinal study has demonstrated that the ability to correctly identify/report spatio-temporal patterns of daily events in first grade was the strongest longitudinal predictor of math skills at the end of grade 2. Notably, these non-numerical ordering skills in this age range were a stronger predictor than numerical ordering skills (i.e., with a semantic magnitude connotation), including order WM, and number ordering tasks. This finding highlights a novel spatio-temporal component of ordinality skills that can be regarded more as domain-general, rather than magnitude-specific, and which seems to be crucial for the appropriate development of math skills at the beginning of formal education. The ability to understand and remember order relationships (e.g., daily events as they occurred) has a strong episodic component, and may be linked to the processing and representations of other spatial and temporal relationships, which are mostly supported by medial temporal lobe brain systems (Buzsáki and Moser 2013; Moser et al. 2008; O'Keefe and Burgess 1996). Specifically, the hippocampus, in the medial temporal lobe, has been systematically associated with successful encoding and retrieval of spatio-temporal contexts (Davachi et al. 2003; Nadel et al. 2000; Rajah et al. 2010; Ross and Slotnick 2008). Hence, the ability to build a strong relationship between spatio-temporal contexts/information—supported by subcortical regions in the hippocampus—may be a precursor/foundation to mathematical learning.

The existence of a spatial (left-to-right ordered) component in the representation of numerical magnitude/numerosity has been supported by the so called Spatial Numerical Association of Response Codes (SNARC) effect (Dehaene et al. 1993), whereas in right-handed subjects responses to numerical judgements for small numbers are faster left-than-right hand, while numerical judgements for large numbers are faster right-than-left hand. This effect has supported the notion of the “mental number line” which postulates that, at least in Western cultures, numbers are spatially represented from left to right (Dehaene et al. 1993). Critically, this association occurs when ordinal information is relevant (i.e., numerical judgements) or irrelevant (i.e., parity judgments on numbers) to the task, suggesting that such spatial component is activated when numbers are presented, independently of the task. Moreover, this spatial coding seems to occur also when subjects are asked to judge non-numerical ordinal information/stimuli such as months and letters, suggesting a similar—or shared—neurocognitive system that processes ordinal information, that is spatially organized (Gevers et al. 2004). Even more critically, a recent study of seven-month olds suggests that mapping ordinal information into a directional space is an early predisposition that precedes language and symbolic knowledge acquisition (Bulf et al. 2017). This datum hints at the idea that a left-to-right spatially organized mental representation of ordered dimensions may be rooted in biologically determined constraints of human brain development (Bulf et al. 2017; de Hevia et al. 2017) and is also observed in newborn chicks (Rugani et al. 2015).

Regardless of the spatial bias that seems to characterize both numerically-relevant and numerically-irrelevant sequences/stimuli, and which likely taps onto a phylogenetically and ontogenetically ancient—and shared (across numerical and non-numerical dimensions)—neurocognitive system, a clear dissociation seems to exist between cardinality and ordinality processes later in development. This may suggest a critical role of experience and schooling on *numerosity coding*. A brain-based dissociation between cardinal and ordinal properties of numbers dates back to the neuropsychological literature whereas a double dissociation has been reported for cardinal and ordinal aspects of numerosities: patient MAR (Dehaene and Cohen 1997) and SE (Delazer and Butterworth 1997) showed intact ordinal but impaired numerical processing, whereas patient BOO (Dehaene and Cohen 1997) and CO (Turconi and Seron 2002) showed the reverse pattern with preserved numerical but impaired ordinal sequence processing. Moreover, in healthy adults cardinality and ordinality judgement tasks have been shown not to correlate with one another—even though both, yet

uniquely, predict math performance (Goffin and Ansari 2016). Further challenging the notion of a common neural substrate for cardinality and ordinality magnitude processing—particularly when stimuli are presented in symbolic format—is the reverse *distance effect*, which has been systematically reported in various studies. The reverse *distance effect* stipulates that judging whether 1 and 2 are in order (either ascending or descending) is faster and less error prone than judging whether 1 and 3 are in order (Turconi et al. 2006; Goffin and Ansari 2016; Lyons and Beilock 2013). This can be interpreted—yet it is only speculative—as a potential failure to inhibit automatically processed counting sequences that are acquired a- semantically—and with a recital component—during early language acquisition (Gelman and Gallistel 1978; Sarnecka and Carey 2008). However, it was also found that ordinality and cardinality predictability accounts of math scores are independent of cognitive control tasks (Goffin and Ansari 2016).

Furthermore, fMRI studies report dissociable networks of activation between symbolic cardinality and ordinality judgements, while their non-symbolic neural correlates were very highly overlapping. Specifically, during non-symbolic judgements, a cohort of typically-developing adult participants showed prominent activation of a fronto-parietal network for both cardinality judgements (i.e., select the larger numerosity among two alternatives) and ordinality judgements (i.e., select whether a given sequence of dots is presented in order or not). Yet, when the symbolic equivalent of such task was presented, participants activated a canonical fronto-parietal network during the cardinality task, while regions of the Supplementary Motor Area (SMA) and pre-SMA were recruited during the ordinality task (Lyons and Beilock 2013). Dissociable neural representations of number symbols have also been reported in perceptual and association cortices. Specifically, it has been shown that the neural similarity between number symbols was positively predicted by the lexical frequency of numerals in parietal and occipital brain areas. By contrast, the similarity space of non-symbolic analogue quantities was positively predicted by the *distance/ratio effect* in prefrontal, parietal, and occipital brain areas (Lyons and Beilock 2018). This seems to support the idea that a failure to inhibit early acquired counting lists may influence similarities and differences of *numerosity codes*, particularly for symbolic stimuli. Hence, while sometimes it is important that the incremental properties of numbers get associated with one other, in other circumstances, and with certain tasks, it may be beneficial to inhibit the phonological/recital aspects of numerical sequencing in order to better access and manipulate its associated cardinality. This notion has important implications for cognitive control theories of numerical and mathematical cognition and development.

Learning to Inhibit Irrelevant Information

So far, we have detailed the basic properties of numbers (i.e., cardinality, ordinality) and their behavioral and neural correlates, as well as described the potential involvement of some executive functions—such as working memory—in the development of these numerosity processes. In this section we will focus on other general neurocognitive processes, which are involved during development and learning of math-related concepts.

For example, learning rules and principles (i.e., the “+” and “-” signs; knowing the bijection and injection functions/properties), and starting to inhibit wrong/intuitive heuristics that do not meet/or do not comply with the formal rule learned, both represent a fundamental milestone of mathematical learning over development (Brookman-Byrne et al. 2018; Houdé and Tzourio-Mazoyer 2003). The highest level of proficiency with numbers lies in (i) the ability to apply different rules given the context (i.e., “+” and “-” signs; flexibility), and (ii) adequately mastering the rules of abstraction. For instance, inasmuch as the perceptual properties of the numerical stimuli—such as size, density, or length—are salient, they do not influence the numerosity of the set and become therefore irrelevant (i.e., they need to be inhibited; Clayton and Gilmore 2015; Gilmore et al. 2016; Houdé and Tzourio-Mazoyer 2003).

Over development, we learn to break away from perception—which relies heavily on automatic and heuristic processes—and to apply learned rules to solve a specific (numerical) problem. This is a process that is supported by inhibitory control regions within the prefrontal cortex, particularly in its ventrolateral aspect, encompassing the anterior insular cortex (AIC) and the anterior cingulate cortex (ACC; Houdé and Tzourio-Mazoyer 2003).

As previously mentioned, certain types of information (i.e., spatial information, but also other magnitude's information such as luminance) can sometimes aid numerical estimation, yet they can also be detrimental when they are yielding conflicting information (Cohen Kadosh et al. 2008) to the numerical task. In the latter case, these types of (redundant) information can interfere with numerical judgements. For example, in a numerical Stroop paradigm, responses are faster when the numerical and size dimensions are congruent with each other (i.e., facilitation); while responses are slower and more error-prone when the numerical and size dimensions are incongruent with each other (i.e., interference; Girelli et al. 2000; Henik and Tzelgov 1982; Rubinsten et al. 2002).

A recent prominent behavioral theory of mathematical cognition has postulated that the relationship between “number sense” and mathematical skills is only significant when the numerical and non-numerical information vary incongruently with each other—e.g., when of two to-be-compared sets the one that has the smaller number of items also has the larger item size or total occupied area and vice versa. This *datum* suggests that inhibitory/cognitive control processes can greatly influence our ability to perform numerical tasks (Fuhs and Mcneil 2013; Gilmore et al. 2013; Viarouge et al. 2023) and, in turn, poor inhibitory control skills may significantly jeopardize adequate mathematical learning. Some studies report that, during number comparison tasks, children with DD are selectively impaired only on incongruent trials and perform adequately on congruent trials (Gilmore et al. 2013; Szucs et al. 2013). Furthermore, in a series of EEG/event-related potential (ERP) studies, Szucs and colleagues demonstrated that, as children progress through education and become more and more proficient with numerical stimuli, brain responses during task-irrelevant trials/stimuli show a signature of weakening interference and strengthening facilitation, suggesting a parallel development of general cognitive control skills and automatic number processing (Soltész et al. 2011; Szucs et al. 2007, 2009).

Critically, over development, other forms of interference emerge that require the aid of neurocognitive inhibitory control mechanisms. This is the case of numerical judgements of decimals-, negative number-, and fraction-like stimuli. School-aged children are likely to think that 1.45 is larger than 1.5 because 45 is larger than 5. In a recent study, it was shown that the ability to compare decimal numbers in which the smallest number has the greatest number of digits, is rooted in the ability to inhibit the learned misconception that the greater the number of digits, the greater the magnitude; and in the ability to inhibit the perceptual input of the length of the decimal number per se (Roell et al. 2017).

The results of these studies converge on the idea that prefrontal cortex mechanisms are essential to mathematical learning at multiple stages of math skills development. Namely, inhibitory control processes—anchored in the prefrontal cortex—are required to keep suppressing irrelevant information, biases, and rules, as a function of the context and the task at hand, prior to number processing becoming the most relevant dimension and starts being automatized.

Furthermore, prefrontal cortex mechanisms may be essential to achieve, through development and training, the ability for numerical abstraction (Cohen Kadosh and Walsh 2009).

Together, the data presented here support the notion of a complex neurocognitive interaction, mediated by prefrontal cortex brain regions that aids the successful development of basic numerical skills.

Mathematical Abilities: Domain-Specific and Domain-General Cognitive Scaffolds

Developing Formal Arithmetic

Thus far, we have shown that some of the foundational building blocks of mathematical knowledge lie in (i) the ability to adequately represent quantities in various connotations and formats, as well as in (ii) being able to “extract” the unique numerosity property of an items set (or of a number) among other perceptual and semantic *biases*. Yet, and as mentioned earlier, when we need to perform arithmetical computations on numbers, other and more sophisticated skills need to be developed. For example, (i) we have to know and understand that adding a number to a set or subtracting an item from a set will affect the numerosity of that set; and (ii) we have to keep track of intermediate results, etc. Notably, approximate forms of these types of arithmetical computations are evident already in infants and toddlers (Barth et al. 2005, 2006; Gilmore et al. 2007; Wynn 1992).

However, complex manipulations of symbolic and abstract quantities (starting from formal counting) require the aid of higher-order cognitive functions that support maintenance of numerical representations in working memory over several seconds. This is achieved through the dynamic interaction of lateral fronto-parietal brain circuits. Critically, the involvement of these working memory circuits changes dramatically with development (Menon 2014). A consistent profile of diminished reliance on lateral prefrontal cortex regions and increased reliance on posterior parietal regions (i.e., the so called “anterior-to-posterior shift”) has been documented in a wide range of studies involving numerical comparisons as well as arithmetical computations (Ansari and Dhital 2006; Ansari et al. 2005; Cantlon et al. 2009). In a seminal study, Rivera and colleagues found that relative to adults, children tend to engage the posterior parietal cortex less, and the prefrontal cortex more when solving arithmetic problems (Rivera et al. 2005), likely reflecting increased specialization and automatization (possibly even through processes of inhibitory control over development; see next section “[Learning to Inhibit Irrelevant Strategies for Arithmetic Problem-solving while Strengthening Arithmetical Representations for Fact Retrieval](#)”). This idea has been supported by arithmetic learning paradigms in adults, which have shown initial prefrontal activation and a shift towards posterior parietal cortex regions as a function of learning and experience (Delazer et al. 2005; Ischebeck et al. 2007). When looking on neurotransmitters in the parietal and prefrontal cortices, it has been shown that neurotransmitters (γ -aminobutyric acid and glutamate) in the parietal cortex explains current mathematical performance and predict future mathematical achievement during childhood, adolescents, and young adulthood (Zacharopoulos et al. 2021b), while mathematical learning, or the lack of it, is related to a neurotransmitter (GABA) in the prefrontal cortex (Zacharopoulos et al. 2021a).

Other studies have more directly addressed the link between working memory abilities and arithmetic skills. For example, Dumontheil and Klingberg found that IPS activity during a visuospatial working memory task predicted arithmetic performance two years later in a sample of six- to sixteen-year-olds (Dumontheil and Klingberg 2012). Further analyses on the neural correlates of individual components of working memory have provided evidence for the fractionation of neurofunctional systems associated with distinct working memory components during arithmetic problem-solving (Arsalidou and Taylor 2011; Metcalfe et al. 2013). Specifically, analysis of the relation between the central executive, phonological, and visuospatial components of working memory, with brain activation during an arithmetic task revealed that visuospatial working memory is a strong predictor of mathematical skills in seven- to nine-year-old children (Metcalfe et al. 2013). This study also demonstrated that visual working memory is associated with increased problem complexity-related responses in left dorsolateral and right ventrolateral prefrontal cortex as well as in the bilateral IPS and supramarginal gyrus (SMG). Notably, visuospatial working memory and the central executive component were associated with largely distinct patterns of brain responses during arithmetic

problem-solving and overlap was only observed in the ventral aspects of the left supramarginal gyrus, suggesting that this region is an important locus for the integration of information in working memory during arithmetic problem-solving in children (Ansari 2008; Dehaene et al. 2003; Kawashima et al. 2004; Kucian et al. 2008; Menon et al. 2000; Rivera et al. 2005).

Finally, analysis of intrinsic functional connectivity suggests that a network of prefrontal and parietal cortical areas supports the longitudinal development of numerical abilities from seven-to-fourteen years of age (Evans et al. 2015).

These findings further confirm the pivotal role of overlapping parietal-frontal working memory circuits in children's mathematical skill development.

Learning to Inhibit Irrelevant Strategies for Arithmetic Problem-Solving while Strengthening Arithmetical Representations for Fact Retrieval

Over development, children's gains in arithmetical skills and mathematical problem-solving is characterized by the gradual replacement of inefficient procedural strategies to more efficient ones. Namely, various counting strategies (i.e., verbal/finger counting) give way to direct retrieval of arithmetic facts (Cho et al. 2011; Geary 2011; Geary and Brown 1991; Qin et al. 2014). This is a process that has been attributed to an initial engagement of the hippocampal subcortical system within the medial temporal lobe and, later, its functional connectivity with lateral fronto-parietal cortical regions (Qin et al. 2014; Rosenberg-Lee et al. 2018). Within this framework, during an addition problem, the association of addend-pairs with their correct solution is first strengthened within the associative learning system residing in the hippocampus. Once such association is made, the so-formed "arithmetical facts" are "transferred" to cortical areas where representations can then "reside" for handy/easy retrieval (Davachi et al. 2003; Qin et al. 2014).

This notion has been validated by a study that implemented a hybrid cross-sectional/longitudinal design, and showed that children's transition from counting to memory-based retrieval strategies over a 1.2-year interval period (i.e., from seven-to-nine to ten-to-eleven year-olds) was mediated by increased hippocampal activation and increased hippocampal-neocortical functional connectivity (Qin et al. 2014). Critically, following an initial increase in hippocampal engagement during middle childhood, this hippocampal dependency decreased during adolescence and adulthood despite further improvements in memory-based problem-solving strategies. This pattern of initial increase and subsequent decrease in activation provides support for the notion that the hippocampus plays a time-limited role in the early phase of knowledge acquisition (McClelland et al. 1995; Tse et al. 2007). The critical, and timely, involvement of the hippocampus in the development of optimal retrieval-based skills was further demonstrated in a training study whereas seven-to-nine-year-old children showed significant increases in hippocampal engagement and hippocampal-cortical interactions following a eight-week arithmetic training (Rosenberg-Lee et al. 2018). Critically, in both studies, changes in subcortico-cortical interactions were paired with increased in fact retrieval strategy-use.

As the representations for arithmetical facts are formed through appropriate cross-talk between hippocampal and cortical systems, those older, inefficient strategies need to be inhibited. This is supported mainly by ventrolateral and ventromedial regions of the prefrontal cortex encompassing the AIC and the ACC.

Critically, weak prefrontal control signals have been associated with worse performance on an arithmetic problem-solving task, both in adults and children (Supekar and Menon 2012). The strength of causal signals from the AIC to ventral parietal and prefrontal regions in the SMG and the ventrolateral prefrontal cortex (VLPFC) respectively, significantly predicted better performance. Furthermore, in adults, an additional link

from the AIC to the ACC has been reported—which significantly and uniquely predicted their performance on the same arithmetic problem-solving task.

Collectively, these results suggest that, over development, together with an anterior-to-posterior functional brain activity shift within the dorsal aspect of the fronto-parietal network (see previous section “[Developing Formal Arithmetic](#)”), a posterior-to-anterior functional brain activity shift in the ventral aspect of the same network may support the development of inhibitory control processes that help to suppress perceptual, or other types of, cognitive heuristics/strategies in favor of more optimal ones. In parallel, subcortical-cortical interactions support the fine-tuning of arithmetical representations in the form of “learned facts.” Together, these processes subtend the development of successful math problem-solving skills.

Intervention

This chapter presents converging evidence for the involvement of multiple brain systems—and the cognitive processes/functions they subtend—to the appropriate acquisition of numerical and mathematical abilities. Thus, it is critical to consider all of them when designing intervention approaches for children that are at the end of the distribution for mathematical and numerical abilities (e.g., children with mathematical learning disabilities (MLD), children with DD). The following section delineates/describes the work that has been done so far on exercising/training/boosting these processes, both at the domain specific, as well as at the domain-general level. These studies’ benefits are two fold: they allow (i) to test whether the above-mentioned neurocognitive mechanisms are causally involved in the development of mathematical and numerical skills, and (ii) to pave the way towards effective interventions in cases of atypical development.

Domain-Specific

Numerosity-Based Interventions

As discussed, numerosity manipulation has been suggested as one of the processes at the core of successful math-knowledge acquisition. Studies on healthy adults, typically developing children and even preschoolers, have shown that numerosity-based training can improve arithmetic performance (Hyde, Khanum, & Spelke, 2014; Park, Bermudez, Roberts, & Brannon, 2016; Park & Brannon, 2013, 2014) – *but see* (Kim, Jang, & Cho, 2018). Hence, numerosity-based interventions have naturally been advocated for the remediation of MLD and DD cases (Butterworth and Yeo 2004). Notably, these interventions have capitalized on symbolic and non-symbolic material and on the use of “numerical manipulatives” (i.e., Cuisenaire rods, number tracks, number cards; Butterworth and Yeo 2004) to aid the learner in forming an accurate representation of (each) numerosity, through active visual manipulations.

Thus far, several training studies have also looked at the effects of software-based learning programs designed to foster active manipulations on numerosities in children with mathematical difficulties. Wilson and colleagues implemented a computer program (The Number Race) specifically designed to train symbolic and non-symbolic number sense through a series of computer-based activities involving counting, and number/magnitude comparisons (Wilson et al. 2006). This study showed only a selected “within-domain” improvement whereas children’s basic numerical (i.e., number sense) skills got better after training, while no significant gains were observed in their arithmetical performance. Similarly, in a study that employed a software program focused on strengthening the mapping between numerosities and their symbolic representations (Graphogame-Math) performance gains were minimal, and so were transfer effects to arithmetical competences (Räsänen et al. 2009).

Critically—and similarly to school-age children with DD—a study on preschoolers at risk for developmental learning disabilities showed that an approximate arithmetic training benefited performance only on early informal, but not formal, arithmetic (Szkudlarek and Brannon 2018).

By contrast, interventions capitulating on visual number-to-space training have shown greater promise. Kucian and colleagues used a custom-made computer-based number-line estimation task (rescue calularis) to train a population of eight-to-ten-year-old children with DD (Kucian et al. 2011). After five weeks' training, improvements were evident on the number line task as well as on an arithmetic task (featuring addition and subtraction problems). Yet, after the training, children with DD still differed in performance compared to their (matched) typically developing peers. Critically, after training, both groups—albeit to a different extent—showed decreases in functional brain activity when performing the number-line estimation task. Specifically, decreases in functional brain activity were evident in regions of the posterior parietal and prefrontal cortices, both critical for numerical manipulations at this age (Ansari and Dhital 2006; Ansari et al. 2005; see also previous section “[Developing Cardinal Skills](#)”). Notably, the results of this study suggest that even though this type of training could not fully rescue performance in the DD group, it could still elicit transfer effects. Most importantly, number-line training induced brain plasticity effects even in the DD group, further highlighting the potential of this approach to treat children with math difficulties. In the wake of these results, other number-based digitalized training programs have been developed that capitalize on the link between non-symbolic and symbolic numerosities onto number lines/tracks (Butterworth et al. 2011; for a review, see also Dowker 2017).

Together, the training studies reviewed here suggest that a number sense training alone may not be sufficient to enhance arithmetical performance, particularly in children at the lower end of the distribution of abilities. In contrast, number-line training was able to elicit some transfer effects, even in children with DD. This indicates that a cognitive training that integrates cardinal as well as visuo-spatial (i.e., ordinal) properties of numbers may aid the developing brain with a more solid numerical representation critical for successful arithmetical performance. In line with this, a recent number sense training study in DD has shown that gains in arithmetic were fully mediated by performance on a visual perception task (i.e., figure matching; Cheng et al. 2020). Indeed, visuospatial processing have long been posited critical for successful mathematical performance (Gilligan et al. 2020; Sella et al. 2016; Verdine et al. 2014).

Yet, it is also possible that other domain-general processes could come to play in mediating this relationship, such as inhibitory processes, or mechanisms of visual attention—which could facilitate performance during visual-form perception and, as such, mediate the relationship between number sense training and arithmetic transfer. More generally, this suggest that to propel significant transfer effects to arithmetical performance, particularly at early stages of development, and in populations who are struggling with math, a number sense training may be accompanied (or should embed) the training of other domain-general processes that could stimulate multiple neurocognitive systems for numerical and mathematical functioning.

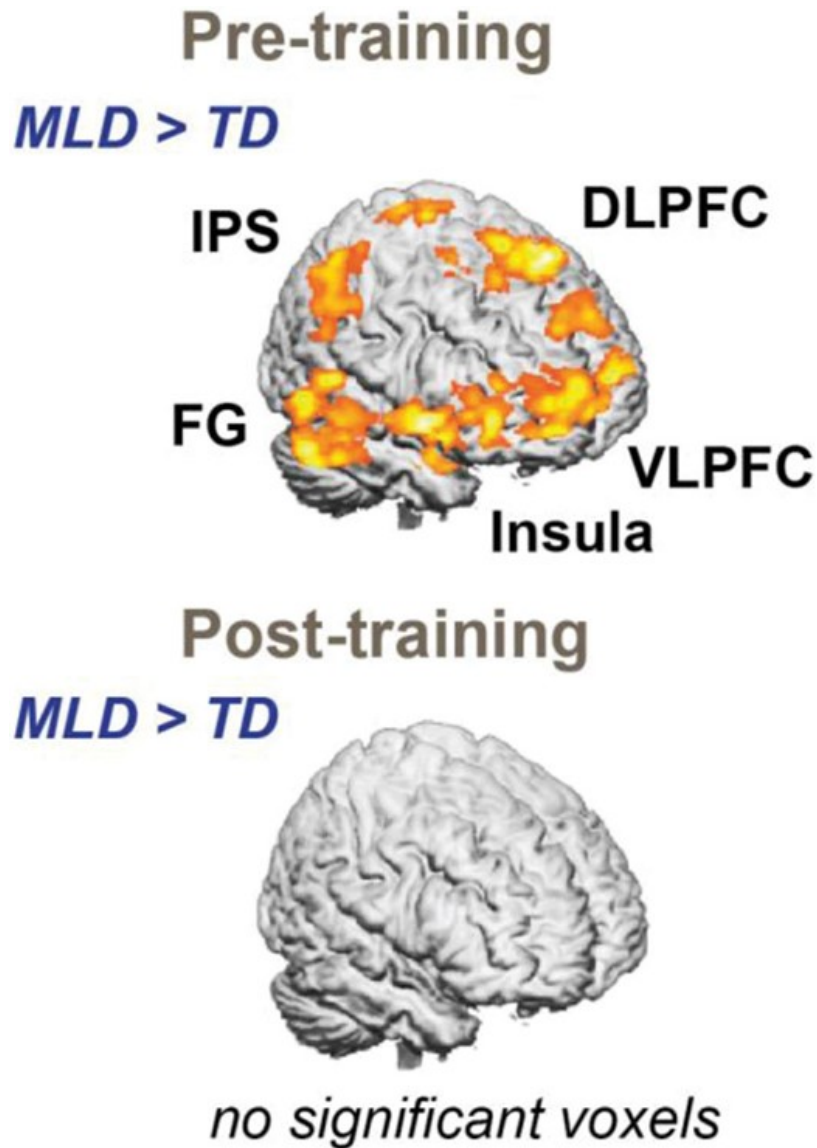
Arithmetic-Based Interventions

A large bulk of studies on the remediation of arithmetical skills are classroom-based intervention studies. These often combine conceptual and procedural activities with speeded practice to strengthen problem-solving skills and promote efficient retrieval of arithmetical facts (Fuchs et al. 2008, 2009; Powell et al. 2009; for a comprehensive review, see Dowker 2005, 2017).

In a recent study, Iuculano and colleagues have looked at the effects—at the brain level—of a comprehensive arithmetic intervention similar to these (Fuchs et al. 2008, 2010; Powell et al. 2009)—yet in a 1:1 setting—on a selected group of children with MLD. The authors showed that, in parallel with performance normalization, eight weeks of 1:1 arithmetic training elicited extensive functional brain

changes in eight-to-nine-year-old children with MLD (Iuculano et al. 2015). This comprehensive arithmetic training normalized aberrant functional responses in the MLD group, to the level of neurotypical peers. Brain plasticity effects were evident in a distributed network of prefrontal, parietal, and ventral temporal-occipital brain regions. Remarkably, machine learning algorithm techniques revealed that brain activity patterns in children with MLD were significantly discriminable from neurotypical peers before training, but statistically indistinguishable after. Notably, changes in brain activity after training in MLD were characterized by significant reduction of widespread over-activation in multiple neurocognitive systems in prefrontal, parietal, and ventral temporal occipital cortices (Figure 2). This suggests that this type of training can induce global changes across distributed brain systems that encompass multiple stages of the information processing hierarchy necessary for successful arithmetic problem-solving (Iuculano and Menon 2018; Iuculano et al. 2018). Specifically, by facilitating the development of quantity representations and the use of sophisticated counting procedures, this type of training might place fewer demands on quantitative and higher-order visual form processes supported by the posterior parietal and ventral temporal-occipital cortices. Concurrently, it might facilitate efficient processing strategies by decreasing load on cognitive neural resources (e.g., working memory, non-verbal reasoning, attention) supported by the prefrontal cortex. More generally, and similarly to what has been discussed before, these findings suggest that a comprehensive training, one which integrates conceptual as well as procedural aspects of arithmetic learning—rather than focusing on isolated components of number knowledge and arithmetic—might be more effective in remediating deficits in multiple neurocognitive systems in children with math difficulties. Critically, it needs be noted that not all children improved after the training. This result calls for a more sophisticated, fine-grained approach for low attainers. Recently, Dowker and colleagues have developed a behavioral protocol for an ad hoc individualized training program—that capitalizes on numerical and arithmetical principles as well as retrieval strategies—and which unfolds as a function of the baseline profile of the child (i.e., Catch Up Numeracy). Notably, behavioral results show significant improvements following this protocol (Holmes and Dowker 2013). The next step will be to implement these types of adaptive arithmetic training programs digitally, as well as test their validity and benefits at the brain level (similar to Iuculano et al. 2015; Kucian et al. 2011). Furthermore, longevity effects are another crucial aspect that needs to be systematically addressed in future studies (see Koponen et al. 2018).

Figure 2:



Neural correlates of arithmetic-based intervention in mathematical learning disabilities.

Top. Before training, children with Mathematical Learning Disabilities (MLD) showed greater functional engagement—during arithmetic problem solving—of multiple neurocognitive systems encompassing prefrontal, parietal, and ventral temporal occipital cortices.

Bottom. Following training, no differences in functional brain activation—during arithmetic problem-solving—were detected between children with MLD and their Typically Developing (TD) peers—adapted from: luculano et al., (2015).

Abbreviations: DLPFC = Dorsolateral Prefrontal Cortex; VLPFC = Ventrolateral Prefrontal Cortex; IPS = Intraparietal Sulcus; FG = Fusiform Gyrus

Domain-General

Executive Functions-Based Interventions

Executive functions are defined as a class of cognitive processes critical to perform goal-directed and purposeful behaviors. They include WM, planning, and cognitive/inhibitory control. We have already discussed the involvement of executive processes in numerical and arithmetic skills acquisition over development. For example, we have seen that functional activity of the IPS during a visuo-spatial WM task significantly predicts subsequent arithmetic performance in a sample of six-to-sixteen year-olds (see previous section “[Developing Formal Arithmetic](#),” Dumontheil and Klingberg 2012; see also Metcalfe et al. 2013). We have also analyzed the importance of cognitive control processes in fostering appropriate numerosity and arithmetic-strategy “tuning” (Soltész et al. 2011; Supekar and Menon 2012; Szucs et al. 2007). Given the involvement of these processes in successful numerical and arithmetical acquisition, we can ask whether cognitive trainings that tap onto these processes can be useful in remediating (or enhancing) math performance over development.

The majority of WM training studies have focused on improving its visuo-spatial component with promising “within domain” results. The most consistently implicated brain correlates of these trainings have been found across regions of the prefrontal and posterior parietal cortices—i.e., the canonical WM network (Constantinidis and Klingberg 2016). Given the involvement of these brain regions (and processes) to math learning and cognition, it has been hypothesized that WM training could lead to significant transfer effects to math performance.

In a cognitive WM training study, Bergman-Nutley and Klingberg tested the effects of a five-week adaptive WM training (Cogmed Working Memory Training Program; Klingberg et al. 2005) on arithmetic fluency in a group of seven-to-fifteen year-olds (the majority of whom suffered from attention deficit hyperactivity disorder (ADHD)). Their results showed improvements on the math fluency test—yet, effect sizes of the improvement were very small ($d = 0.2$), particularly when compared to other cognitive abilities assessed: visual-WM, and the ability to follow instructions ($0.67 < d < 0.90$) (Bergman-Nutley and Klingberg 2014). As previously discussed, given that math competency is the result of the interaction of multiple neurocognitive systems and abilities, minimal transfer effects following a visuo-spatial WM training alone are not surprising.

A better approach may be to train multiple executive functions (EF) simultaneously. A recent study has indeed combined a comprehensive training of EFs in a group of primary school children and assessed its effects on academic outcome measures. Training occurred for ten weeks and, similar to Klingberg and colleagues (2005), was also adaptive. The authors report changes in multiple facets of EFs, including inhibitory control, flexibility, as well as on school grades of reading and math (Goldin et al. 2014). Even though this study had no imaging component, it provides preliminary (and corroborating) evidence for the unique benefits of comprehensive training protocols for strengthening math competencies over development.

Embodied-Based Interventions—A Proxy to Foster Ordinal Skills and Spatial Information

This line of research capitalizes on the fact that the development of accurate numerical representations could be fostered by bodily sensory (and motor) experiences. In a recent series of studies, Nuerk and colleagues showed that kindergardeners that were trained to solve a magnitude comparison task on a digital dance mat demonstrated significant improvements on a number-line estimation task, as well as on a subtest of a standardized mathematical achievement battery (TEDI-MATH) (Cress et al. 2010). Notably, improvements of the “dance-mat group” were greater than those of a control group trained on the same magnitude comparison task—and for the same amount of time—but using a personal computer. Similar results were found when training first-graders to indicate the position of a given number by walking to the estimated location on a number line on the floor (Link et al. 2013).

At the brain level, the dorsolateral prefrontal cortex (DLPFC) seems to be a key player in this process. The DLPFC has a pivotal role of integrating multiple forms of information in WM, allowing for flexible (and accurate) mental representations (Prabhakaran et al. 2000). Notably, transcranial direct current stimulation (tDCS) of the DLPFC during a number-line training involving body movements along a physical line was shown to improve performance in a group of healthy adult participants. Improvements were seen on the number-line task (trained), as well as on a WM task (untrained). Critically, training effects were specific to the experimental group that received DLPFC stimulation combined with bodily mental number-line training, and lasted up to two months after training (Looi et al. 2016). Similarly, transcranial random noise stimulation (tRNS) over the bilateral DLPFCs combined with a similar mental number-line bodily training improved learning and performance of children with MLD (Looi et al. 2017). Notably, training gains correlated positively with improvement on a standardized math test, and this effect was strengthened by tRNS.

We would like to emphasize that we do not aim to provide a comprehensive review of the intervention literature in this field (for a more comprehensive review on this topic, see Dowker 2005, 2017). However, all in all, the studies reviewed here suggest that cognitive trainings designed to “stimulate” multiple aspects of math knowledge (and the neurocognitive systems subtending it) may yield the best outcomes to significantly improve (or remediate) arithmetical skills—particularly in individuals falling at the lower end of the distribution of abilities.

Conclusions and Future Directions

In this chapter, we report on how numerical and mathematical cognition is developed from a neurocognitive perspective. Such development is associated with quantitative and qualitative changes in multiple brain networks, as well as the involvement of a myriad of cognitive processes that can be considered both domain-specific and domain-general. We reviewed these multiple distributed neurocognitive systems, which are involved in quantity manipulation, perceptual (coding and decoding, inhibitory control, and working) and associative declarative (memories), as well as the corresponding brain regions and networks that support and orchestrate the development of numerical and mathematical cognitive skills. The involvement of these neurocognitive processes and systems is complex, dynamic, and, most importantly, a function of development, proficiency of skills, and the task at hand. While we have focused on positive findings, it is important to note that not all the studies find a support that domain-specific (e.g., numerosity) or domain-general (e.g., working memory) are involved in mathematical ability (van Bueren et al. 2022), and further studies should examine the effects due to experimental settings, educational systems, and culture. In addition, while we focused mainly on fMRI, it is important to acknowledge other approaches that could allow more comprehensive understanding of brain development and its link to mathematical development, such as neurotransmitters, metabolic changes, or aperiodic brain activity (van Bueren et al. 2022). Further research in developmental cognitive neuroscience can foster our understanding of the involved neurocognitive mechanisms as a function of age in typical and atypical populations, providing the required knowledge to design and promote effective interventions at the cognitive and neural levels.

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