Magnitude Processing in Developmental Dyscalculia

A Heterogeneous Learning Disability with Different Cognitive Profiles

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Abstract

Developmental dyscalculia (DD) is a learning disability that is characterized by severe difficulties with acquiring age-appropriate mathematical skills that cannot be attributed to insufficient education, language skills, or motivation. The prevalence rate is estimated at 3-6%, meaning that a substantial portion of the population struggles to learn mathematics to such a large degree that it affects overall well-being and academic prospects. However, our understanding of the etiology of DD is incomplete and there are competing hypotheses regarding the characteristics of DD and its underlying causal factors. The purpose of the current thesis is to contribute to our understanding of DD from the perspective of cognitive psychology and cognitive neuroscience. To this end, we identify children with DD to identify the cognitive determinants of DD that hamper their ability to learn basic mathematics. It is believed that human beings are endowed with an innate ability to represent numerosities, an ability phylogenetically shared with other species. We investigate whether the purported innate number system plays a role in children with DD insofar as failures in this system may undermine the acquisition of symbolic representations of number. Although some researchers believe DD is a monolithic learning disability that is genetic and neurobiological in origin, the empirical support for various hypotheses suggests that DD may be shaped by heterogeneous characteristics and underlying causes. The present thesis, and the studies presented therein, provides support for the notion that DD is indeed heterogeneous. We identify at least two subtypes of DD that are characterized by specific deficits in number processing, and one subtype that could more aptly be labelled as a mathematical learning disability, the causal factors of which are likely limited to deficits in non-numerical abilities. In addition, we locate candidate neurocognitive correlates that may be dysfunctional in DD.

List of papers

The thesis is based on the following research papers.

I. Skagerlund & Träff (2014). Development of magnitude processing in children with developmental dyscalculia: space, time, and number. *Frontiers in Psychology*, 5:675.

II. Skagerlund & Träff (2016). Number Processing and Heterogeneity of Developmental Dyscalculia: Subtypes with Different Cognitive Profiles and Deficits. *Journal of Learning Disabilities*, 46(1), 36-50.

III. Träff, Olsson, Östergren, & Skagerlund (submitted). Heterogeneity of developmental dyscalculia: Cases with different deficit profiles

IV. Skagerlund, Karlsson, & Träff (submitted). Magnitude processing in the brain: an fMRI study of time, space, and number as a shared cortical system

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Introduction

In contemporary society, we are always surrounded by numbers. No matter where we look, there are symbols carrying important pieces of information. For example, we may consult our watch or our smartphone to estimate whether we have to run to catch a bus. After identifying the correct bus number, we may have to use our credit card to pay for our bus ticket. Moreover, there are the various PIN numbers and passcodes that we need to remember for numerous activities and services that are now part and parcel of modern life. One of humanity's greatest cultural innovations is mathematics. The principles of mathematics allow us to reason with numbers, to calculate, and to enumerate quantities. The basic principles of adding, subtracting, dividing and multiplying are ubiquitous in all aspects of our lives; we calculate when grocery shopping, paying our bills, reading recipes, formulating scientific ideas and so on. Being fluent with numbers is therefore imperative to function successfully in western civilization.

Failure to acquire adequate mathematical abilities may severely hamper one's prospects of career success as well as one's physical and mental well-being (Butterworth, 2010; Kucian & von Aster, 2015). There are numerous reasons why individuals may not acquire sufficient mathematical competency. The factors that have been linked to low numeracy are insufficient education, low socio-economic status, and cognitive dispositions.

In the general population, approximately 3-6 % (Kucian & von Aster, 2015) of school children show profound difficulties in gaining sufficient numeracy. These children show difficulties that cannot be attributed to their intelligence, language ability, or attention. Mounting evidence suggests that this group of individuals suffers from a severe learning disability called *developmental dyscalculia* (DD). Despite the relatively high prevalence rate, there is a surprising lack of consensus in the academic and educational community regarding the mechanisms and causes underlying its development. Some argue that DD is a monolithic disability that is caused by a neurocognitive dysfunction (e.g., Piazza et al., 2010) in a specific number system in the brain, whereas others contend that DD is heterogeneous in nature and may arise for multiple different reasons (Rubinsten & Henik, 2009).

Purpose and aim

In this thesis, I investigate the nature of DD from a cognitive psychological perspective. I also incorporate methods and findings from cognitive neuroscience, with the ambition of gaining a comprehensive understanding of DD at multiple levels. The questions that I want to address are: How can we characterize DD? What are the causes of DD? Is DD truly a homogeneous learning disability? What are the cognitive processes involved in performing mathematical computations, both in DD and in normal children, and what neurocognitive substrates subserve them? These overarching questions and goals are far too complex to be addressed within a single project. Nevertheless, these goals, distantly located on the horizon, inspire an attitude in which we can anchor and focus lower-level goals that relate to the above questions. My hope is that we can make some progress, no matter how limited, in understanding DD. More specifically, one aim is to identify children with DD and tease out the underlying cognitive abilities and processes that subsequently undermine their ability to acquire numerical competency. Is it a missing affinity with symbolic numbers that give rise to mathematical difficulties in this population? Or is it the underlying semantic representations of quantity that are impaired? How do more domain-general cognitive abilities, such as working memory and executive functions relate to this learning disability? Moreover, is the innate ability to represent numerosity specific to numerosity alone, or is it better conceived of as being part of a more generalized magnitude system (e.g., Walsh, 2003)? The goal is ultimately to be able to implement targeted interventions in educational settings, and one step towards this goal is to investigate the aforementioned questions. In the following sections, I will elaborate on what we currently know about the cognitive processes involved in mathematics, how the brain processes this information, and the current state of knowledge with respect to the etiology of DD.

Mathematical cognition

Mathematics is a scientific discipline that is concerned with problem-solving in accordance with certain axioms targeted at investigating the relationship between quantities and spatial structures. Embedded within mathematics there are several subdisciplines, such as arithmetic, algebra, calculus, geometry, and trigonometry. The most basic of these subdisciplines is arithmetic, which is concerned with formal operations upon quantities. These operations are ubiquitous during education in the elementary school system, in which children are taught the principles of addition, subtraction, division and multiplication. Performing successful calculations according to these procedures requires a basic affinity with numbers, which are written using Arabic notation in the Western world, and the underlying quantities, which are expressed in the base-10 system. The symbolic system, consisting of Arabic numerals and verbal number words, and the underlying quantities provide the foundation for arithmetic and more complex mathematical operations. The field of mathematical cognition is concerned with understanding the underlying neurocognitive processes that enable and constrain the acquisition of mathematics competency (Dehaene, 2011). The following sections will elaborate on what we currently know about the cognitive processes involved in performing mathematical computations and the underlying neural substrates of the brain subserving them.

The science of mathematical cognition – a disclaimer

If one wants to understand how human individuals gain mathematical competency and understand why some children have such a hard time learning basic arithmetic skills, there are several possible targets for investigation. One could try to understand the role of the teacher and pedagogy behind mathematics learning, one could explore mathematics itself—the subject-matter—and discern why some aspects of math are harder than others, or one could focus on the learner. Additionally, it cannot be stressed enough that an overall understanding of how mathematical abilities are acquired and what gives rise to difficulties in understanding math is an enormously complex endeavor. A complete understanding requires, among other things, in-depth analyses of societal factors (e.g., how families' socio-economic status affect learning opportunities), social factors (e.g., how the social climate in classroom settings affect learning outcomes), and cognitive factors (e.g., how individual cognitive abilities such as intelligence and language affect learning). Thus, mathematics learning can—

and should—be understood at multiple levels of analyses. Nevertheless, my thesis is firmly rooted at the lowest of these levels, the cognitive level. One could arguably continue even lower, where one might study the influence of neurocognitive or even genetic factors on the ultimate disposition of mathematics learning. I am sympathetic to the assumptions of cognitive neuroscience and recognize the importance of the genetic and neurocognitive factors discovered in that field. Therefore, the empirical work put forward in this thesis is directed at the level of the individual, and I employ methods and assumptions from cognitive psychology and cognitive neuroscience. One such assumption is that cognitive processes, in the form of mental transformations and computations, are realized by underlying neural processes in the brain and that cognitive processes are inherently about information-processing (Neisser, 1967). Thus, our understanding of mathematical cognition is guided by constraints and characteristics at both the neural level and cognitive level and the *explananda*, in which we are interested, can be understood and measured at either of these levels. Researchers within cognitive psychology often employ a chronometric methodology (i.e., measuring response times) or response accuracy to understand the complexity of any given cognitive process. These also offer measures of how any given individual performs relative to a population or sample mean. These measures are targeted at the cognitive level (but inferred from *behavioral data*), whereas analytical tools in cognitive neuroscience (such as fMRI, with which brain activity patterns can be measured) are concerned with how these same cognitive processes are realized at the neural level in the brain. Thus, given that both cognitive psychology and cognitive neuroscience share the same theoretical assumptions about cognitive processing, they have a bidirectional relationship in which they inform and complement each other’s efforts to understand cognitive phenomena in an integrative, multidisciplinary approach (Aminoff et al., 2009). Ultimately, our goal is to understand how these neurocognitive processes relate to higher-level behavior, such as mathematical abilities. This will allow us to determine whether DD can be derived from an underlying neurocognitive dysfunction, and if it does, this insight will provide initial guidance for devising appropriate interventions that address the cognitive characteristics of this condition.

Dots and digits: Basic number processing and mathematics

Even though formal mathematics is a sophisticated cultural artefact, the mechanisms supporting mathematical thinking are believed to be evolutionarily ancient in origin and not unique to humans. This section will elaborate on these basic number processing systems, which can be incorporated under the general term *number sense* (Dehaene, 2011), and how they may relate to Arabic numerals. Together, these systems comprise the foundation for basic arithmetic and higher mathematical thinking.

The Approximate Number System

Mathematics is, at its core, concerned with the relationship between quantities and spatial structures. Although formal mathematics relies heavily on symbolic representations and complex rules that are uniquely human, it is believed that human beings are endowed with a very basic and innate capacity to apprehend and manipulate quantities in an approximate manner (Dehaene, 2011; Halberda, Mazzocco, & Feigenson, 2008; Piazza, 2010). This approximate number system (ANS) is phylogenetically shared with other species, such as monkeys, rats and pigeons (Brannon, Jordan, & Jones, 2010). The evolutionary rationale for the emergence of the ANS across species is that it may allow animals to perceive and represent quantities in the environment that are important for survival. For instance, foraging and hunting are vital activities that require the apprehension, and perhaps discrimination, of one or more sets of important objects in the immediate environment. Empirical support for the notion of an inborn ability to represent and discriminate between quantities comes from research on infants, in which Xu and Spelke (2000) demonstrated that 6-month-old infants could reliably discriminate between 8 and 16 objects. However, Xu and Spelke (2000) also found that these infants could not discriminate between 8 and 12 items, which points to a quintessential trait of the ANS: its inherent noisiness (Feigenson, Dehaene, & Spelke, 2004). Mounting evidence supports the notion that the ANS is noisy and that this noisiness is due to its logarithmic nature. That is, larger numbers are represented closer together than smaller numbers. This means the accuracy of number discrimination and apprehension of quantities varies as a function of the magnitude and ratio between sets (Bugden & Ansari, 2011;

Dehaene, 1992; Feigenson et al., 2004; de Hevia et al., 2006). However, the ability to reliably discriminate between sets of objects develops throughout ontogeny, as individuals can make finer discriminations of decreasing ratio differences as a function of maturation and experience (Halberda et al., 2008; Xu, & Spelke, 2000). Halberda and Feigenson (2008) demonstrated that 3-year-olds could discriminate 3:4 ratio arrays, while 5-year olds could discriminate 5:6 ratios. Acuity of the ANS increases until it reaches a peak in adulthood, at approximately 20 years of age, at which point adults generally show an ANS acuity that allows discrimination of a 9:10 ratio (Libertus & Brannon, 2010; Piazza, 2010). The point at which individuals can make reliable discriminations between sets, in terms of the ratio between sets of objects, provides an index of ANS acuity. In addition, research has showed that ANS acuity adheres to psychophysical laws and can be understood in terms of Weber's law. Thus, the ANS acuity of any given individual can be computed by calculating a Weber fraction (Halberda et al., 2008). This yields an index of how much a set of objects must increase in relation to another set for an individual to reliably notice a difference (Halberda, et al., 2008, Libertus, Feigenson, & Halberda, 2011).

The idea that the ANS is inherently noisy, and the conceptualization of the ANS in general, is also congenial with some interesting and robust effects found in empirical studies. The so-called *distance effect* (Moyer & Landauer, 1967) can be observed when participants are asked to determine which of two simultaneously presented Arabic numerals is the largest. The distance effect refers to the fact that the choice of the larger of two numerals is faster when the numerical distance between numerals is large compared to small. For instance, participants generally respond faster when comparing numerals with a larger distance between them (e.g., 3 vs. 8) than with a smaller distance (e.g., 3 vs. 4). Another interesting phenomenon, *the problem size effect* (Dehaene, Dupoux, & Mehler, 1990; Moyer & Landauer, 1967), refers to the observation that the selection of the larger of two numerals is performed faster when the numerals are small (3 vs. 4) than when they are large (9 vs. 8). Together, these two effects demonstrate that the magnitude representations underlying symbolic numerals are mentally represented as approximate analogue magnitudes and fit nicely with the conceptualization of the ANS. It is hypothesized that this ability to represent and manipulate quantities may constitute the foundation for the symbolic number system used for learning formal arithmetic (e.g., Dehaene, 2011; Gallistel & Gelman, 2000). As young children develop language and a language-based symbolic number system (i.e., counting words and digits), it is believed there is a mapping of the counting words and visual symbols onto the innate number system (Starkey and Cooper, 1980; Gallistel & Gelman, 2000). However, there is an ongoing debate regarding the exact relationship between the ANS and formal mathematics and the relationship between the affinity with symbols and the innate ANS. Nevertheless, mounting evidence consistently shows that there is indeed a relationship between ANS acuity and mathematics performance (e.g., Chu, vanMarle, & Geary, 2015; Halberda et al., 2008; Libertus et al., 2011; Mazzocco, Feigenson, & Halberda, 2011). One suggestion is that the ANS may facilitate children's early understanding of cardinal values and acquisition of number knowledge (Chu et al., 2015). Interestingly, children with DD often display poor ANS acuity compared to their peers, which has led researchers to hypothesize that DD is caused by a deficit in the preverbal number sense that subsequently hampers the subsequent acquisition of numerical competency (Mazzocco, et al., 2011; Piazza et al., 2010). I will elaborate more on this issue in a later section.

Parallel individuation and the object-tracking system (OTS)

The ANS is part of our inborn capacity to represent and manipulate quantities, but the ANS is only capable of approximating larger numerosities in an analogue fashion and is not involved in representing the exact number of objects. Evidence suggests that humans are equipped with a second system called the *object tracking system* (OTS) or *parallel individuation system* that is responsible for the identification and representation of a limited number of objects (typically 1-4; Piazza, 2010). The OTS and parallel individuation system will henceforth be treated as interchangeable constructs. The OTS enables us to keep track of objects in our environment and separate them as distinct individuals throughout space and time. Moreover, this system seems to be linked to visuospatial short term memory (Piazza, 2010) and attention (Hyde, 2011) and permits the quick identification of a small number of objects through a process called *subitizing*. Subitzing refers to our ability to quickly and accurately assess small number of quantities (Kaufman, Lord, Reese, & Volkmann, 1949) as opposed to serial counting or estimation (Ashkenazi, Mark-Zigdon, & Henik, 2012). Subitizing is readily observable in reaction time data from tasks that require participants to verbally indicate how many dots are present in a visually presented array of objects. For objects ≤4 participants respond correctly almost instantaneously without error, whereas for objects >4 the response curve increases dramatically in slope (Piazza, 2010). This suggests that there are at least two dissociable systems involved in counting and that these systems are partly specialized for a specific range of numerosities. Whereas the ANS continues to develop into adulthood and become more refined, development of the OTS occurs rapidly and plateaus by 12 months of age (Hyde, 2011). Further support for a dissociation between the ANS and OTS comes from neuroimaging and neurophysiological data, which indicate that the OTS relies more on inferior parts of the posterior parietal lobe and the occipital lobe, whereas the ANS is primarily subserved by neurocognitive correlates in the right intraparietal sulcus (IPS; Hyde & Spelke, 2011; Xu & Chun, 2006).

Numerosity coding – a third system?

Butterworth (2010) proposed a somewhat different account of how the innate number system works. The *numerosity coding* account of number processing holds that numerosity is represented and processed differently than other continuous quantities. In this model, mental representations of numerosities are believed to be represented as discrete sets of neuron-like elements in an exact manner (Butterworth, 2010). Thus, unlike the conceptualization of the ANS, in which the ANS represents quantities approximately, the numerosity coding hypothesis posits that human beings are endowed with a number system that can represent larger sets exactly in terms of numerosity, much like the OTS for smaller numbers. The feasibility of this account is supported by neural network modelling (Zorzi & Butterworth, 1999; Zorzi, Stoianov, & Umiltà, 2005). Neuron-like elements, such as nodes in a hypothetical neural network, are devoted to semantic representations of numerosities in a one-to-one fashion. For example, processing of the numeral “4” elicits activation of four distinct neural elements that thus constitute “fourness”, while processing of the numeral “2” elicits activation of two separate neural elements and captures the concept of "twoness". It is argued that the ANS and OTS are not sufficient to support arithmetic skills because according to Butterworth (2010), they would not allow for consistent and accurate arithmetic calculations above the small number range. The ANS would not be sensitive enough to be able to handle arithmetic operations, such as $n + 1$, where n is any numerosity above the subitizing range. The inherent noisiness of the ANS may render the solution of this operation undetectable and thus necessitates a conceptualization of number processing that can support exact number processing, such as the numerosity code (Butterworth, 2010).

The relationship between symbols and numerosities

Even though the issue of whether there are two or more dedicated systems for the processing of numerosities is an open empirical question, there is a general consensus that there must be some type of mapping between symbols and their underlying magnitude (e.g., Dehaene, 2011; Feigenson et al., 2004; Gallistel & Gelman, 1992; Gelman & Butterworth, 2005; Piazza, 2010; Starkey & Cooper, 1980; Wynn, 1992; 1995; Xu & Spelke, 2000). Given that human beings are equipped with an innate preverbal sense of numerosity before acquiring a symbolic number system, which must be learned, clues about the relationship between symbolic and non-symbolic number systems can be found in work within developmental psychology. The symbolic number system can be expressed in two different codes (Dehaene, 1992): (1) a verbal word code, in which children initially learn to associate specific small quantities to their auditory symbolic referent, and (2) a visual code which is most commonly associated with written Arabic numerals and is mastered later in ontogeny (Dehaene, 1992). Together with the innate number system, which may be considered an internal analogue magnitude code, these systems comprise the basic components of the so-called *triple code model* of number processing (Dehaene, 1992). This model has received considerable empirical support (e.g., Dehaene, Piazza, Pinel, & Cohen, 2003; Schmithorst & Douglas Brown, 2004), and there is little disagreement that young children learn to associate verbal number words with quantities well before understanding written Arabic notations (Fayol & Seron, 2005). There is disagreement, however, over whether acquisition of the symbolic number system is supported by the OTS or the ANS. Carey (2009) put forward the idea of *bootstrapping*, which explains how an affinity with small numbers, such as 1-4, supported by the OTS or parallel individuation system, provides the foundation for understanding the counting sequence and the successor function ($n + 1$). Children first understand that adding one item to a set leads to a new cardinal value that is labeled by another word further away in the counting list. This leads to the understanding of exact numbers, which is only later connected with the ANS, according to Le Corre and Carey (2007). The idea of bootstrapping also fits nicely with the apparent developmental hiatus of the development of number knowledge that can be observed in young children. By the 2nd year, young children begin to understand that number words refer to numerical quantities. They quickly learn the numbers 1-4, after which there seems to be a delay of several months before they move on to the next numbers (Wynn, 1992), which may indicate that bootstrapping is taking place. However, as Piazza (2010) notes, there is little reason to expect a delay at all for numbers 1-4 given that the OTS has already matured by 12 months of age. Thus, a second account of how children acquire an understanding of symbols has been proposed. Given that the ANS is inherently noisy and is subject to maturation throughout development, small numbers, such as "1" or "2", can be represented very early in development, whereas larger numbers, such as "4" or "5", cannot. Thus, to understand the number "3", children need to be able to reliably distinguish between "3" and "2", and to understand "4", children need to distinguish between "4" and "3" and so on. This developmental pattern fits nicely with the trajectories observed by Wynn (1992), and thus the ANS may support and constitute a foundation for the acquisition of the symbolic number system (Piazza, 2010). The distance effect and the problem-size effect can be observed during symbolic tasks, such as digit comparison, where participants have to decide which of two numerals is the largest. This indicates that the symbolic system, consisting of Arabic numerals and number words, relies on representations that are analogous in nature, which supports the notion that decoding numerals elicits underlying magnitude representations in the ANS (Dehaene, 2011; Piazza, 2010). Geary (2013) proposed that children acquire *number knowledge* in a three-step process, in which the ANS forms the foundation and initial step after which a numeral-magnitude mapping takes place and results in explicit number system knowledge. The speed and efficiency with which this knowledge is formed is driven by domain-general cognitive abilities, most notably attentional control and intelligence (Geary, 2013). Thus, to understand mathematical cognition we must also understand how these general cognitive abilities contribute, which will be the subject of the following section.

Beyond numbers: General cognitive abilities and mathematics

The previous section highlights that arithmetic and mathematics rely on very basic number processing mechanisms and systems. However, the acquisition of mathematical competency likely depends on several cognitive abilities that are subserved by distributed neurocognitive networks (Fias, Menon, & Szücs, 2013). It is also likely that different constellations of cognitive abilities contribute differently to different aspects of mathematics (e.g., Fuchs, et al., 2010; Träff, 2013). The relative importance of these different cognitive abilities may also change depending on ontogenetic factors as well as educational factors (Meyer, Salimpoor, Wu, Geary, & Menon, 2010). Therefore, in this section, I will elaborate on the domain-general cognitive abilities that have been proven to be important for mathematical skill acquisition and performance.

The role of memory

Given that mathematics is inherently about formal operations upon quantities according to certain principles, such as addition and subtraction, successful execution of these operations relies on memory processes. Semantic long-term memory (Geary, 1993) and working memory (e.g., Bull, Espy, & Wiebe, 2008; Swanson & Beebe-Frankenberger, 2004; Szücs, Devine, Soltesz, Nobes, & Gabriel, 2014) are crucial during mathematical reasoning (Meyer et al., 2010). Baddeley and Hitch (1974) formulated the now widely accepted working memory model that comprises three main components. The three components are (1) the phonological loop, which handles acoustic and verbal information; (2) the visuospatial sketchpad, which is mainly concerned with visual and spatial information; and (3) the central executive, which is an attentional control system that monitors and allocates attentional resources and executes tasks. All of these components are relevant during mathematical problem-solving. In fact, each component has been linked to mathematical ability, but studies suggest that the relative contribution of each working memory component differs depending on the type of mathematical task used as an index of mathematical ability (Fuchs et al., 2010). The phonological loop allows for the maintenance of verbal information, such as arithmetic information presented orally to a problem solver, and studies suggest that verbal WM is a predictor of mathematical ability when word problems are part of the mathematics assessment (Fuchs et al., 2005). Written calculations, however, draw on visuospatial WM capacity to a greater extent, and Passolunghi and Lanfranchi (2012) report that visuospatial WM is more predictive of mathematical proficiency overall than the phonological loop. Meyer et al. (2010) studied a sample of children in 2nd and 3rd grade and found evidence of a developmental shift in reliance on different working memory components. The authors found that phonological loop performance predicted achievement in 2nd grade, whereas visuospatial abilities predicted mathematical achievement in 3rd grade. Meyer et al. (2010) argue that this shift can be attributed to neurocognitive maturation and practice. They also highlight the role of the central executive in the early stages of learning, which will be the topic of the next section.

Executive functions and attention

The ability to maintain effortful attention, while ignoring both internal and external distractions, allows some children to learn more quickly than their less attentive classmates (Engle, Kane, & Tuholski, 1999). Geary (2004) suggests that the central executive is involved in facilitating the selection of appropriate strategies during mathematical problem solving and in allocating attentional resources during strategy execution. In addition, Kaufmann (2002) suggests that it supports children's acquisition of novel procedures and their development of automatic access to facts (Kaufmann, 2002; Lefevre et al., 2013). The central executive has been linked to mathematical achievement (Lefevre et al., 2013; Meyer et al., 2010), especially among younger children (Henry & MacLean, 2003). Although the conceptualization of the central executive is debated, one way of assessing it is by administrating tasks requiring participants to shift between tasks while inhibiting distracting elements. Performance on this type of task has proved to be a strong predictor of mathematical achievement (Szücs et al., 2014). Meyer and colleagues (2010) argue that executive attention is especially important during the early stages of mathematics learning prior to neurocognitive maturation, after which mathematical procedures and knowledge becomes more automatized and reliant upon areas in the parietal cortex.

Intelligence and logical reasoning

The specific role of intelligence in acquiring mathematics proficiency is currently debated, but Geary (2013) argues that intelligence is primarily important during the early stages of learning the systematic relations among numerals. In particular, intelligence could facilitate the learning of the mental number line. A large longitudinal study of more than 70,000 children found that intelligence accounted for 59 % of the variance in mathematics scores (Deary, Strand, Smith, & Fernandes, 2007). Further empirical support for the importance of general intelligence, as measured by performance on Raven's Progressive Matrices (Raven, 1976), was provided by Kyttälä and Lehto (2008), who found that general intelligence predicted math achievement in a sample of ninth graders. Thus, intelligence seems to be important throughout the educational career of both younger and older children. Morsanyi and Szücs (2015) argue that mathematics and logical reasoning, which is an important aspect of intelligence, are fundamentally related. Both mathematics and logical reasoning requires that an individual retrieves and applies normative rules and draws correct conclusions from given premises (Morsanyi & Szücs, 2015). Previous research has established a bidirectional relationship between mathematics and logical reasoning skills. For example, Attridge and Inglis, (2013) found that education in mathematics improved logical reasoning skills, and Morsanyi, Devine, Nobes, and Szücs (2013) found that children with superior mathematical abilities excelled in logical reasoning.

Language ability

Early development of number skills and rudimentary arithmetic skills depends on language and phonological skills (Dehaene, 1992; von Aster & Shalev, 2007). For example, language allows children to verbally count objects in their environment, which is the first numerical activity that children overtly perform (Sarnecka, Goldman, & Slusser, 2015). Language and the verbal labels of counting words enable children to acquire and understand the principles of counting, such as ordinality and cardinality (Gelman & Gallistel, 1978; Sarnecka et al., 2015). Language and phonological processing are also involved in more sophisticated aspects of mathematics. According to the triple code model (Dehaene, 1992), the verbal-phonological code is used when establishing and retrieving arithmetic facts, and research suggests that reading skills and phonological processing contribute to early mathematical development (Hecht, Torgesen, Wagner, & Rashotte, 2001). De Smedt, Taylor, Archibald, and Ansari (2010) reported that phonological awareness predicted success in solving arithmetic problems even when controlling for reading ability. However, discrepant findings have been reported by Moll, Snowling, Göbel, and Hulme (2015), who found that phonological awareness did not predict arithmetic skills when both oral language ability and executive functions were included in their models. Nevertheless, the authors highlight the role of language and executive functions in early arithmetic skills in children. The importance of language in early mathematics attainment is also emphasized by Lefevre et al. (2010). They utilized a longitudinal design and showed that language at age 4.5 years was more predictive of formal arithmetic at age 7.5 years than a measure of quantitative knowledge (Lefevre et al. 2010). Thus, language plays an integral role in the acquisition of early number knowledge and early arithmetic skills. Throughout ontogeny, however, that role seems to diminish and is gradually replaced by visuospatial abilities (cf. Meyer et al., 2010).

Spatial processing

Several aspects of mathematics focus on visual representations and their magnitudes and relations, such as geometry and trigonometry. In addition, education and instruction often rely on visuospatial tools and strategies (Fias, van Dijck, & Gevers, 2011). It is, therefore, not surprising that spatial processing is intimately tied to learning mathematics. However, the link between mathematics and spatial processing does not seem to be restricted to sophisticated aspects of mathematics, such as trigonometry. Rather, it seems that space and numbers are intimately related in a very basic sense (Fias et al., 2011). It has also been argued that numbers are mentally represented along a horizontal left-to-right line called *the mental number line*. Preliminary support for this notion comes from self-reports of students who claim that they mentally navigate along a horizontal ruler when solving mathematical problems (Fias et al., 2011). Robust empirical support for the association between space and numbers can also be found in the shape of a now-classic effect. Intriguingly, individuals tend to make decisions regarding smaller numbers more quickly when the response button is located to the left and higher numbers when the response button is located to the right (Moyer & Landauer, 1967). This effect has been named the *Spatial-Numerical Association of Response Codes* (SNARC; Dehaene, Bossini, & Giraux, 1993). Thus, number-space mappings are not only a visuospatial tool that students exploit when solving arithmetical problems; rather, the mental representation of magnitudes, such as numerosity, is inherently spatial (Fias et al., 2011).

Explicit links between spatial processing and mathematical achievement have also been investigated (e.g., Gunderson et al., 2012). Zhang et al. (2014) found that spatial visualization skills predicted arithmetical achievement, and Szücs and colleagues (2014) argue that the role of spatial skills is more important for mathematics than basic number processing or 'number sense'. Gunderson et al. (2012) found that mental rotation ability predicted the linearity of number line knowledge. The researchers suggest that spatial ability plays an important role in mathematics by helping children to develop a meaningful linear mental number line (Gunderson et al., 2012). They also found that spatial skills at age 5 predicted approximate calculation skills at age 8, thereby establishing a direct link between spatial skills and arithmetic (see also Hegarty & Kozhevnikov, 1999). Lefevre and colleagues (2010) conducted a longitudinal study that revealed that spatial attention was strongly related to number naming and the processing of numerical magnitude.

Mathematics and the brain

A central assumption within cognitive psychology and cognitive neuroscience is that the brain and its underlying architecture of neurons and their connections, is the medium through which cognitive processing is achieved. Researchers within the field of mathematical cognition share this assumption, and with the rapid technological advances that have been made in recent years, we are beginning to understand the neurocognitive mechanisms subserving mathematical thought. Thus, to understand how human beings are able to engage in and learn (or fail to learn) mathematics, we must also understand how the brain works. Although much remains to be discovered about how the brain processes mathematics, researchers have begun to map the various areas involved and their specific functional roles. The following sections will elaborate on what we know so far.

Number processing in the brain

Neuropsychological studies in which lesions in the parietal cortex gave rise to severe difficulties with performing mathematical operations were the first to identify the importance of this region for numerical and arithmetic processing (e.g., Dehaene & Cohen, 1997; Delazer & Benke, 1997). As mentioned previously, human beings share an innate ability to apprehend and manipulate quantities in an approximate manner using the ANS with other animals and non-human primates. This ability and its neurocognitive correlates are beginning to be mapped in the human brain because of recent advances in neuroimaging techniques (e.g., Ansari, 2008), and research indicates that there is a primate homologue in the posterior parietal cortex (Nieder & Miller, 2004), further supporting the notion of a shared evolutionary heritage. There is now a general consensus that the IPS plays a crucial role in number processing and mathematics overall (e.g., Ansari, 2008; Dehaene et al., 2003; Butterworth, Varma, & Laurillard, 2011; Kaufmann, Wood, Rubinsten, & Henik, 2011) This cortical area is heavily implicated in all types of arithmetical and numerical tasks, suggesting that the IPS is the core cortical structure for mathematical capacities (Butterworth et al, 2011). Using a high field fMRI, Harvey, Klein, Petridou, and Dumoulin (2013) found a topographic representation of numerosity in the right IPS, where neural populations were sensitive to a preferred numerosity and tuning width. This is consistent with studies of macaque neurophysiology that have found single neurons in the posterior parietal cortex that are sensitive to specific numerosities (Nieder, & Miller, 2004). Transcranial magnetic stimulation (TMS) is a noninvasive technique that can induce temporary disruptions along the surface area of the cortex by altering the firing rate of neurons. Cohen Kadosh et al. (2007) used this technique on healthy subjects, which induced DD-like symptoms on number processing tasks when administered near the right IPS. Thus, it is increasingly clear that the IPS represents non-symbolic magnitudes and may form the basis for more complex mathematical feats.

Neuroimaging studies have also investigated which areas that are involved in symbolic number processing. Researchers have hypothesized that the IPS would be activated irrespective of notation (Arabic numerals, words, dots) in conjunction with the areas devoted to decoding symbols (e.g., Pinel, Dehaene, Riviére, & LeBihan, 2001). Evidence from neuroimaging corroborates this idea, as researchers have found activation in the IPS bilaterally during both non-symbolic number discrimination and symbolic number discrimination in both adults (Nieder & Dehaene, 2009) and children (Cantlon, Brannon, Carter, & Pelphrey, 2006). In addition, activation of the IPS was modulated by the distance of the magnitudes being compared, hence replicating the behavioral distance effect at a neural level. Thus, the IPS is believed to be the ontogenetic neuronal origin for processing the basic semantics of numbers (Bugden & Ansari, 2015). Although both children and adults activate the IPS during number processing, adults seem to activate a more posterior part of the IPS, which has been interpreted as reflecting maturation and increased automatization of number processing (Kaufmann et al., 2011). By contrast, children activate a more anterior part of the IPS as well as additional frontal areas of the cortex, which has been attributed to imprecise and immature number representations. Thus, eliciting frontal areas may be a sign of compensatory mechanisms in children (Ansari, 2008).

Although many studies report overlapping brain areas underlying the processing of both symbolic and non-symbolic magnitudes, numerous neuroimaging studies consistently point to more ventral areas of the parietal cortex as being specifically tuned to symbolic processing (e.g., Holloway, Price, & Ansari, 2010; Price & Ansari, 2011). The angular gyrus (AG) is thought to be essential for grapheme-to-phoneme transformations (Horwitz, Rumsey & Donohue, 1998; Joseph, Cerullo, Farley, Steinmetz & Mier, 2006) and is therefore a likely candidate for symbolic number processing. Indeed, Price and Ansari (2011) found that simply viewing and attending to Arabic numerals elicited activation in the left angular gyrus (AG). Wu et al. (2009) found stronger AG activation when participants solved arithmetic problems written in Arabic notation than Roman notation, indicating the AG is involved in storing overlearned facts, such as symbols and their referents. Additionally, the supramarginal gyrus (SMG), located in the ventral parietal cortex, has been found to be involved in symbolic number processing. For example, Polk, Reed, Keenan, Hogarth, and Anderson (2001) reported a case with a lesion in the SMG who was selectively impaired in symbolic but not non-symbolic number processing. Although this claim is disputed (cf. Park, Li, & Brannon, 2014), others have also found that frontal areas, such as the inferior frontal gyrus (IFG), encode symbolic information (e.g., Nieder, 2009), and researchers also report symbolic distance effects that modulate activation in the IFG (Ansari, Garcia, Lucas, Hamon & Dhital, 2005).

In a neuroimaging study of young children, Park et al. (2014) performed a psychophysiological interaction (PPI) analysis, which yielded insight into the functional connectivity of neural populations in the brain, and found conjoint activations of the right parietal cortex and left SMG during symbolic number processing. The SMG has been found to be involved in phonological storage and production (Henson, Burgess & Frith, 2000) and may play a role in orthographic-to-phonological conversion (Price, 1998). Thus, the effective connectivity from the right parietal cortex to the left SMG may represent verbal mediation of the conversion of Arabic numerals to their numerical magnitudes. The degree of connectivity was negatively correlated with age, which might indicate a reduction in verbal mediation with development. As children become more fluent in symbol-to-number mapping, they may rely less on verbal mediation. This interpretation is consistent with the idea that the representation of number in the Arabic form depends on the verbal system at the initial learning phase but quickly becomes independent of verbal coding (Fayol & Seron, 2005), instead becoming increasingly automatized (Park et al., 2014).

Performing calculations

The cortical areas involved in basic number processing, such as the IPS and the AG, constitute the foundation for more complex cognitive processes called upon during mathematical reasoning and arithmetic. So, what are the additional neurocognitive mechanisms allowing for advanced calculations? Solving mathematical problems requires an intricate orchestration of different neurocognitive processes linked in overlapping distributed networks in the brain (Fias et al., 2013). The first step in solving any hypothetical, visually presented mathematical problem is to decode the visual information and recognize that the scribblings are in fact Arabic numerals. The visual word form area in the left occipitotemporal cortex is involved in identifying words and letters from the feature level prior to association with phonology and semantics (Dehaene & Cohen, 2011), after which the identified numeral is associated with its underlying numerical quantity through concurrent IPS activation (Fias et al., 2013). Studies using more complex problems have shown a fronto-parietal network comprising the IPS and the AG in the parietal cortex and frontal areas, such as when solving arithmetic problems with larger operands (Grabner et al., 2007). Calculating and solving problems with smaller operands relies relatively more on AG activity and less on the frontal areas, a fact that has been attributed to the use of verbally stored arithmetic facts that can be retrieved effortlessly (Grabner et al., 2009). In a similar vein, researchers have observed a developmental shift in cortical activity subserving mathematical computations, whereby children rely more on the frontal areas. Throughout ontogeny, as they hone their mathematical skills, children gradually shift to more posterior activation patterns around the IPS and AG (Rivera, Reiss, Eckert, & Menon, 2005). One interpretation is that young children initially have to rely significantly more on working memory and attention during problem solving. As they become more proficient, they gain the ability to retrieve arithmetic facts from memory, which consequently reduces the cognitive load on working memory and attention (Rivera et al., 2005). Research has also identified the hippocampus as being involved during arithmetic problem solving in children together with frontal regions, which indicates that hippocampal regions may be important for establishing arithmetic facts (Cho et al., 2012).

In sum, engaging in successful arithmetic problem solving depends on a complex neurocognitive network, involving several areas distributed across the brain (see Fig. 1 below for an overview). It is also important to be aware of the fact that there is a developmental shift in cortical activation patterns subserving mathematical cognition, which underscores the need for systematic investigations across the entire spectrum of ontogeny to fully understand mathematical cognition in general and DD in particular.

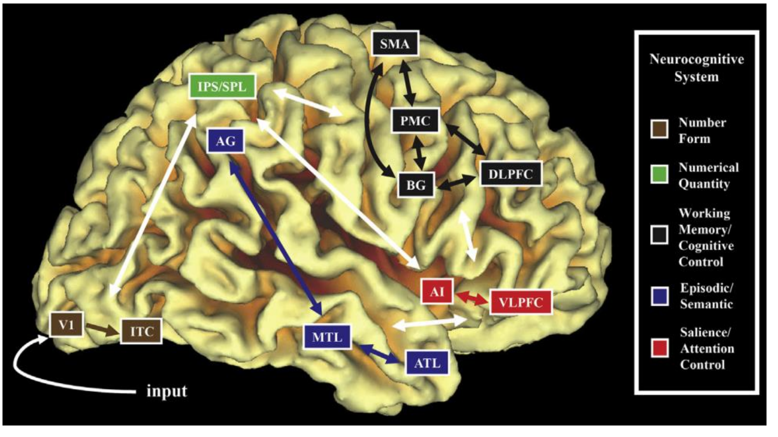

Figure 1. A model of the neurocognitive circuitry involved in mathematics (Fias, Menon, & Szücs, 2013). Some areas are more directly involved in mathematics (e.g., the IPS in the parietal cortex) and some are indirectly involved (e.g., visual areas in the occipital cortex). The indirectly involved areas are not discussed fully in the main text.

Time, space, and number – a magnitude system in the brain?

Numerosity can be considered to be a continuous dimension (i.e., more than-less than) and is omnipresent in the human environment. Time and space are two additional ubiquitous and continuous dimensions of human existence. Being situated in the physical world involves the occupation of a given spatial locus at a specific given time and trying to reason about the current state of the world from available percepts. Thus, successful cognitive and sensorimotor activity has to account for and bind these concepts and representations. Recognizing this, Gallistel and Gelman (2000) argued that a countable quantity (discrete numbers) and uncountable quantity (mass quantity variables, such as amount, area, and time) should be represented with the same type of representations in order to be combined and used for important decisions for the individual. Walsh (2003) proposed, in his *A Theory of Magnitude* (ATOM), that human beings possess a shared core system for these different magnitude representations and that these abilities have a common neural correlate in the human brain. What does this have to do with mathematics and developmental dyscalculia? People with DD often complain about having an impaired sense of time (Cappelletti, Freeman, & Butterworth, 2011). Indeed, Vicario, Rappo, Pavan, & Martino (2012) found that eight-year-olds with DD have a weak time discrimination ability compared to controls. Visuospatial deficits are often reported in children with DD. Given the potential deficits in processing other magnitude dimensions, this suggests that an understanding of how the brain processes magnitudes in general may provide important insight into the etiology of DD.

Mounting evidence suggests that these dimensions are interrelated at the behavioral level (for a review, see Bonato, Zorzi, & Umiltà, 2012). Explicit behavioral links between space and quantity, for example, can be found when looking at the distance effect mentioned previously, the phenomenon that shows that the further apart two numbers are, the easier one finds it to compare them (Dehaene, 2011). The discovery of the SNARC effect also inspired research that found other interactions. Ishihara, Keller, Rossetti & Prinz (2008) found an interaction between space and time, in which time is also represented on a left-right dimension or “mental time line”; this interaction is now aptly called the “Spatial-Temporal Association of Response Codes” (STEARC) effect. In a similar vein, when individuals are asked to estimate the duration of visually presented numerals, they tend to underestimate smaller numerals and overestimate larger numerals, showing a time and number interaction – now called the *Time-Numerical Association of Response Codes* (TiNARC) *effect* (e.g., Kiesel & Vierck, 2009).

Researchers from various disciplines have now congregated with the ultimate goal of understanding the nature of this apparently shared magnitude system, addressing questions concerning the degree of neurocognitive overlap (or independence) across dimensions (e.g., Agrillo & Pfiffer, 2012; Fabbri, Cancellieri, & Natale, 2012; Hayashi et al., 2013; Vicario, Yates, & Nichols, 2013). As with processing of numerosity, spatial processing, such as evaluating line length and mentally rotating objects, has been linked to neurocognitive correlates in the IPS (Fias, Lammertyn, Reynvoet, Dupont, & Orban, 2003; Jordan, Wüstenberg, Heinze, Peters, & Jäncke, 2002; Milivojevic, Hamm, & Corballis, 2009). Milivojevic et al. (2009) found a linear increase of activation in the dorsal IPS with angular rotation on a mental rotation task, as well as activation in the supplementary motor area (SMA). These areas in the parietal cortex have also been found to be involved in temporal processing (e.g., Wiener, Turkeltaub, & Coslett, 2010). Researchers have also highlighted prefrontal areas, such as the IFG and SMA (Wiener et al., 2010) in addition to the inferior parietal cortex (Bonato et al., 2012; Lewis & Miall, 2003; Wittman, 2009). Insight into the potentially shared magnitude system has been provided by Dormal, Dormal, Joassin, & Pesenti (2012), who utilized two tasks pertaining to two different magnitude dimensions in their neuroimaging study. They reported that a temporal task and a numerosity task elicited common activation patterns in a large right-lateralized fronto-parietal network, including the IPS and areas in the frontal lobe (Dormal et al., 2012).

In sum, these findings provide converging evidence for the existence of a shared magnitude representation that is localized in the IPS, which may form the foundation for mathematical cognition.

Investigating neurocognitive processes in the brain using fMRI

The insights into the neural correlates described above are the products of non-invasive neuroimaging techniques, primarily using fMRI. To appreciate and understand the possibilities and limitations of these techniques, and in light of the fact that study IV in this thesis utilizes fMRI methodology, I will give a brief overview of the fMRI technique and what exactly it measures in the following section.

Cognitive processes are assumed to be instantiated by the electrochemical activity of neurons, and functional neuroimaging techniques, such as fMRI and positron emission tomography (PET), are important tools that can be used to understand these cognitive processes (e.g., Cabeza & Nyberg, 2000; Henson, 2005). The fMRI technique does not measure neural activity directly, but rather uses hemodynamic fluctuations in the brain as a proxy for neural activity. When neurons are activated, they metabolize glucose and oxygen supplied by the surrounding vascular system. Oxygenated blood is supplied to the active population of neurons, after which the nutrients are metabolized, resulting in deoxygenated hemoglobin. Oxygenated and deoxygenated hemoglobin have different magnetic properties; deoxygenated hemoglobin is paramagnetic and is thus attracted to magnetic fields. This fact is used in fMRI, in which the proportion of oxygenated and deoxygenated blood is measured using strong magnetic fields and gives an index of neural activity. This technique is called blood-oxygenation-level dependent (BOLD) contrast and is how we measure neural activity in response to tasks performed in an fMRI scanner. Images of the entire brain are collected in slices of volumetric elements ("voxels"), each capturing the BOLD signal, that together form a complete brain volume. One brain volume is typically captured every 2-3 seconds and constitutes a complete 3D representation of all of the voxels, with each volume comprising approximately 100 000 voxels. The signal intensity of each voxel is then analyzed for statistical differences, much like any dependent variable in experimental psychology (Henson, 2005), between different conditions of the fMRI paradigm. There are two primary ways of presenting stimuli in an fMRI experiment: blocked design or event-related design. A blocked design involves a sequential presentation of several trials within a block, or epoch, where the BOLD response is continually measured over the entire block. Each block can last approximately 30 seconds. One experimental block is then followed by a resting period and a subsequent control block that is used as a contrast. This design is powerful insofar as it maintains the hemodynamic response over the entire block and therefore allows for strong BOLD signals and statistical power (Friston, Holmes, Price, Büchel, & Worsley, 1999). In an event-related design, each trial is matched to an image acquisition, which allows for analyses of individual responses to trials. For example, this allows for specific analyses of the hemodynamic response pertaining to correct or incorrect trials (Amaro & Barker, 2006), but it also requires that the hemodynamic response returns to baseline for each trial, making it time consuming.

One simple way of investigating the neural correlates for any given cognitive task is to compare two conditions, such as an experimental condition and a control condition, by subtracting the BOLD contrast from a control condition from the BOLD contrast from an experiment condition. This subtraction analysis gives information about the processing underlying a specific task, albeit in a somewhat rudimentary manner, and can be used in more advanced analyses (Amaro & Barker, 2006). Nevertheless, the description here captures the gist of the methodology that we use to investigate neurocognitive processes in the brain.

Developmental Dyscalculia

Developmental Dyscalculia is a mathematical learning disability that is characterized by a severe selective impairment in acquiring numeracy that cannot be attributed to poor instruction, reading skills, motivational factors, or intelligence (Butterworth, 2005). The literature of mathematics difficulties, in general, is riddled with confusing terminology, and there are indeed many different reasons why one might have difficulty in learning mathematics and performing mathematical operations (Kaufmann et al., 2013). It is estimated that, in the UK, 22% of adults have such a great difficulty with mathematics that it causes practical and occupational limitations (National Center for Education Statistics, 2011). However, only a small portion of those adults can likely be identified as having DD; in fact, the prevalence rate of DD is estimated to be approximately 3.5 to 6 % (Rubinsten & Henik, 2009; Shalev, 2007), which is about the same rate as dyslexia. The modern conceptualization of DD can be traced back to Kosc (1974), who suggested that DD is a genetic and congenital learning disorder, a belief still held today (Butterworth, 2010). Kosc (1974) also introduced a discrepancy criterion to evaluate whether someone should be considered to have DD. The discrepancy criterion stipulates that the mathematical attainment demonstrated by a child does not match the IQ level of that child. The discrepancy criterion has been widely used in clinical settings until recently, and only with the introduction of the *Diagnostic and statistical manual of mental disorders* (5^{th} ed.; DSM-V; American Psychiatric Association, 2013) has this criterion been abandoned. The discrepancy criterion has an initial appeal but was removed from the DSM-V to recognize the fact that individuals with lower IQ scores also can suffer from DD; this change facilitates the diagnosis of such individuals. Along with dyslexia, the specific term “dyscalculia” was removed from the DSM-V and is now referred to as “Specific Learning Disorder” with a set of diagnostic criteria, such as “Difficulties mastering number sense, number facts or calculation (…)” and “Difficulties with spelling (…)”. The purpose of this maneuver was to give the clinician more flexibility and to account for the high comorbidity rate of dyslexia and DD. It was not an attempt to discredit either dyslexia or DD as a learning disorder. So what are the characteristics of DD and what are the causes? This is the topic for the next section.

Characteristics and potential core causes of DD

A predominant view of DD has long been that it is a congenital condition that is genetic in origin and affects the innate ability to mentally represent and manipulate quantities (Butterworth, 2005; Dehaene, 2011). In turn, this disruption makes learning basic mathematics very difficult. In this vein, the etiology of DD has been conceptualized as being caused by a core deficit in the ANS (Mazzocco et al., 2011; Piazza et al., 2010) that subsequently hampers acquisition of the symbolic system. Studies have shown that children with DD have a higher Weber fraction, the index of ANS acuity measured using number discrimination tasks. For example, Piazza et al. (2010) found that 10-year-old children with DD performed on par with 5-year-old children without DD. Mazzocco and colleagues (2011) found similar results, but they also made additional comparisons to a group of low achievers, typical achievers and high achievers in mathematics. These comparisons indicated that only the DD group (< 10^{th} percentile) had dimished ANS acuity, whereas the low achievers (11^{th}-25^{th} percentile) demonstrated an intact number sense. This supports the notion that DD is not a graded phenomenon along a continuum, but rather that the children in the bottom end of the achievement spectrum constitute a qualitatively distinct category of children with severe mathematics disabilities. This also suggests that the cognitive deficits and causes of those difficulties are likely different than for children with less severe difficulties (i.e., low achievers). These findings also underscore the importance of being wary of how samples are composed in terms of percentile scores, and great care should be taken not to conflate different groups with different cognitive profiles (Mazzocco et al., 2011).

Another study by Desoete, Ceulemans, De Weerdt, and Pieters (2012) followed a sample of children from kindergarten to 2nd grade and found that non-symbolic number ability was predictive of arithmetic achievement one year later and that children with DD in 2nd grade showed impaired performance on both non-symbolic and symbolic number processing in kindergarten. The results from neuroimaging studies corroborate the idea that DD can be traced to a core deficit in the ANS: children with DD have demonstrated abnormal activation patterns in the right IPS during numerical processing (Ashkenazi, Rosenberg-Lee, Tenison, & Menon, 2012; Price, Holloway, Räsänen, Vesterinen, & Ansari, 2007; Rykhlevskaia, Uddin, Kondos, & Menon, 2009).

A related core deficit account of DD has been proposed by Butterworth (2005; 2010) who argues that the deficit is not due to a dysfunctional ANS but rather to problems in the coexisting system for representing numerosity in an exact fashion. Incidentally, this system is also subserved by neurocognitive correlates in the IPS, and DD is characterized by difficulties with the exact enumeration of sets and not with the approximations of sets. Empirical support has been provided by Landerl, Bevan, and Butterworth (2004), who found that 8-to-9-year-old children with DD performed worse than age-matched controls on a dot counting task. Iuculano. Tang, Hall, and Butterworth (2008) extended those findings and found that children with DD did not have any difficulties with tasks requiring manipulating approximate numerosities or approximate calculations. However, exact enumeration was compromised (Iuculano et al., 2008).

It is worth noting that enumeration tasks require the participant to give oral responses, which are inherently symbolic in nature, so the fundamental problem may be in accessing the semantic content when decoding symbols. Thus, children with DD may not have a deficit in the innate numerosity-coding system but rather a persistent disconnect between symbols and their referents. Rousselle and Noël (2007) have proposed such an account of the underlying cause of DD, which they call the *access deficit hypothesis*. This hypothesis states that DD is related to problems not with processing numerosities but rather with accessing magnitude information from symbols (i.e., numerals). Thus, the main causal element in DD is the connection between symbolic numbers and pre-existing magnitude representations (Rousselle & Noël, 2007; Noël & Rousselle, 2011). Observations from a developmental perspective support this hypothesis. Noël and Rousselle (2011) provide an overview of studies investigating DD at different ages and observe an emergent pattern indicating that deficits in symbolic and exact number representations seem to precede observed impairments in the ANS. Symbolic deficits are present at ages 6-7, with unaffected ANS acuity (De Smedt & Gilmore, 2011; Rousselle & Noël, 2007), whereas impaired ANS acuity is only demonstrated in samples of children aged 10 and above (Piazza et al., 2010; Price et al., 2007; Mazzocco et al., 2011). One interpretation is that aberrant symbolic number processing might undermine the maturation of the ANS representations in DD, leading to impaired non-symbolic approximate number processing later on (Noël & Rousselle, 2011).

Instead of advocating a domain-specific "core" hypothesis of DD, some researchers have argued that domain-general cognitive abilities are implicated in the learning disability (e.g., Geary, 2004). Early research into mathematical learning disabilities (MLD), a more general notion of mathematics difficulties encompassing a wider performance spectrum (e.g., < 25th percentile), have consistently found aspects of working memory to be dysfunctional (Geary, Hoard, Nugent, & Bailey, 2012; McLean & Hitch, 1999; Swanson, 1993). A deficit in visuospatial attention has been suggested to be a potential cause of DD because of its essential role during arithmetic processing (Geary, 2004). Children with mathematical difficulties committed more errors than their IQ-matched peers when solving multistep arithmetic problems (Russel & Ginsburg, 1984). These errors may be caused by spatially misaligning numbers when writing down partial answers or while performing carrying or borrowing procedures. These mathematical errors may also be the result of a poor regulation of attentional resources by the central executive component of working memory (Geary, 2004). In that vein, some researchers posit that DD may be attributable to dysfunctional executive functions (Ashkenazi & Henik, 2010; Szücs, Devine, Soltesz, Nobes, & Gabriel, 2013). Szücs and colleagues (2013) found that children with DD performed worse on inhibition tasks and visuospatial WM tasks, which they argue is the core deficit of DD. The researchers argue that aberrant IPS morphology in DD is likely not a biomarker of a dysfunctional ANS, but instead is indicative of dysregulation of executive functions and visuospatial processing (Szücs et al., 2013). This conclusion is supported by research that points to the IPS and nearby cortical areas as responsible for attentional processes and visuospatial processes such as mental rotation (Jordan, Wüstenberg, Heinze, Peters, & Jäncke, 2002; Kucian et al., 2007).

Thus, each hypothesis described above has received some empirical support from both behavioral and/or neuroimaging studies. Although perplexing at first, there are a number of different interpretations of these discrepant and seemingly incompatible results (cf. Kaufmann et al., 2013). First, researchers have used different screening criteria, both in terms of indices of mathematical abilities and percentile cut-offs, to define DD. Second, researchers have used different ways of assessing the putative construct in question. For example, ANS acuity can be measured using slightly different task setups. Third, the discrepant results may also be a consequence of inconsistent control of comorbidity, such as ADHD and dyslexia, and other cognitive abilities. Finally, and most notably, it may be that DD is not a homogeneous learning disability with a single etiological cause as previously thought. Thus, it is plausible that DD is heterogeneous and that the observed phenotypes might be caused by a multitude of underlying neurocognitive causal factors (Kaufmann et al., 2013; Rubinsten & Henik, 2009) giving rise to subtypes of DD. The idea that there are subtypes of DD is not new and can be traced as far back as Kosc (1974) and more recently to Geary (2004) and the more neurocognitively grounded work by Rubinsten and Henik (2009). The idea that there are subtypes of DD will be the topic of the next section.

The many faces of DD – subtypes and heterogeneity

Geary (2004) observed different behavioral patterns in children with DD during mathematical problem solving. Some children with DD resort to age-inappropriate finger counting strategies, even during rudimentary calculations, which Geary (2004) called the *procedural* subtype. These children also make procedural errors and show a poor understanding of concepts. Children with the second DD subtype show difficulties in retrieving mathematical facts for simple arithmetical problems in terms of both speed and accuracy. This group of children is referred to as the *semantic memory* subtype. The children in the last subtype, the *visuospatial* subtype, are prone to errors when engaging material that is spatially represented and when reasoning about mathematical relationships (Geary, 2004). Later research has targeted lower-level cognitive processing, such as basic number processing, to disentangle the potential heterogeneity of DD (e.g., De Visscher & Noël, 2013; Iuculano et al., 2008). In a case study of two boys with DD, Iuculano and colleagues (2008) found that one child's performance pattern was suggestive of an access deficit subtype, whereas the other child had difficulties with non-symbolic numerosities. Another case study by De Visscher and Noël (2013) of a 42-year-old woman diagnosed with DD demonstrated severe impairments in retrieving arithmetic facts. A comprehensive evaluation of her basic number skills and cognitive abilities indicated that she did not have any difficulties in basic number processing; however, extensive testing of her long-term memory revealed a hypersensitivity to interference, which prevented her from establishing an arithmetic facts network.

Instead of using case studies to unravel cognitive profiles of individuals with DD, one research team used cluster analysis to identify subtypes (Bartelet, Ansari, Vaessen, & Blomert, 2014). The authors examined a large sample (N = 226) of children with DD on a comprehensive test battery, which included basic number processing tasks as well as tasks tapping domain-general cognitive abilities. The cluster analysis generated six clusters:

I. This cluster had problems with number line estimation tasks

II. This cluster had problems with approximate numerosities and number line estimation tasks.

III. This cluster showed similar problems as cluster II as well as an additional weakness in visuospatial working memory capacity.

IV. This cluster was characterized by weak symbolic number processing.

V. This cluster had no number processing impairment and no weakness in cognitive abilities. Interestingly, this cluster showed strong verbal working memory.

VI. This cluster was characterized only by lower nonverbal IQ.

The cluster analysis is compatible with each hypothesis previously described. Cluster II and III are likely caused, at least partly, by a dysfunctional ANS. Cluster IV is compatible with the access deficit hypothesis. Cluster V is surprising, but a tentative interpretation is that the arithmetic impairment in this subgroup can be attributed to exogenous factors, such as poor motivation or education (Bartelet et al., 2014).

Given this apparent heterogeneity, different researchers have independently proposed that the academic community should distinguish between *primary DD* and *secondary DD* (Kaufmann et al., 2013; Price & Ansari, 2013). Price and Ansari (2013) suggest that primary DD denotes a subtype that is characterized by more severe arithmetical difficulties derived from a congenital disposition undermining the ability to process numerical magnitude. Secondary DD denotes a subtype of children with less severe arithmetic difficulties where the pathology is not attributed to numerical magnitude (Price & Ansari, 2013). These two subtypes correspond well with the distinction between DD children and low achievers (LA), as shown by Mazzocco et al. (2011). Price and Ansari (2013) suggest that primary DD is driven by endogenous neurocognitive factors pertaining to number processing, whereas secondary DD is driven by external factors. Kaufmann and colleagues (2013) suggested a similar distinction, but provided a more specific definition of secondary DD, where the numerical deficits could be explained entirely by non-numerical impairments, such as attention or working-memory processes (Kaufmann et al., 2013).

Empirical studies

Overarching aim

The primary aim of this thesis is to enhance our understanding of the etiology of DD. The aim involves the identification of defining characteristics in terms of the cognitive processes that underlie the demonstrated learning deficits in children with DD. There are several hypotheses regarding the origin of DD, and one ambition is to investigate each of these and disentangle whether DD is truly a homogeneous disability with a single core deficit that is responsible for its etiology. A secondary aim is to gain a better understanding of the neurocognitive correlates of number processing and to investigate whether humans are endowed with a domain-general magnitude system, of which the ANS may be part.

General method

To investigate the cognitive characteristics and underpinnings of DD, we used different approaches in the four studies. In this section I will describe the general method used in terms of participant recruitment and overall study designs. I will also lay out some definitions and descriptions of the tests and abilities that they measure. The procedure for each study varied substantially and is therefore briefly described in the summary of the papers.

Design

We used different designs across studies targeted at different levels of analyses that answered slightly different research questions. Cross-sectional designs were used in study I and II, where groups of children classified as having DD were compared to at least one control group. Cross-sectional designs are efficient in terms of the amount of time required to collect data; however, making group comparisons in a quasi-experimental design inherently limits the inferential power regarding the extent and direction of causality. Therefore, in study I, we employed a second control group consisting of younger, ability-matched children that would provide additional insight into the developmental trajectory of cognitive abilities in children with DD. In study III, we utilized a case study design that allowed for further investigation of the findings in study I and II. The type of group analyses that were made in those first studies gives important information in terms of the models (i.e., population means) that describe the targeted population according to some variable. Thus, findings about how children with DD perform on various variables provide rough estimates of behavior that are assumed to capture and represent all of those individuals putatively included in the target population. Irrespective of the accuracy of those models, we wanted to obtain more fine-grained data by honing in on single individuals with DD to determine how viable those models are at the level of the individual. Educational interventions are usually inferred from group data, but the implementations are themselves targeted at the individual level. Therefore, there is a need for investigations beyond group analyses alone, hence the case study design of study III where four children with DD were given an extensive test battery aimed at elucidating the cognitive profile of these children to determine whether our group models can be extrapolated and applied to the single individual child. The aim of study IV was to investigate the neurocognitive correlates of the generalized magnitude system (i.e., ATOM) and to investigate the degree of overlap across dimensions. To this end, an fMRI paradigm was developed and the study used a within-subjects alternating block design.

Participants with DD – identification and subtyping

Researchers studying DD rarely have the opportunity to study individuals with a clinical diagnosis of DD, at least not in large groups, but instead have to rely on screening procedures and cut-off criteria where the sampling relies on probabilities. Thus, given that calculated estimates of DD points to a prevalence of 3.5 to 7% in the general population, researchers often choose cut-off criteria of scores on standardized tests or norms near this interval to identify children with DD. This is somewhat suboptimal because this procedure is vulnerable to including false positives in the sample, and support and corroboration should be provided through replications and complementary research approaches. Nevertheless, to minimize the likelihood of including children in the DD groups that do not belong to that population, several precautions and steps were undertaken in our studies. First, in the studies that included children with DD (Study I, II, and III), we initially contacted teachers in special education, who were then asked to identify children who demonstrated specific difficulties in mathematics and who received special instruction mathematics. In addition, the same teachers were asked to disregard children who showed signs of having difficulties with attention or other neurologically based conditions, such as dyslexia. Second, children who were ultimately classified as DD also had to perform below a certain cut-off criterion on a set of tests measuring mathematical ability. The cut-off was different between studies (7.5th percentile in study I, 5th percentile in study II, and 10th percentile in study III) due to the use of different screening tasks. Measures of general intelligence and reading ability were also used, either as inclusion criteria or as covariates in ANCOVAs. The children were recruited from 27 different schools from around Östergötland region. The age of the children differed across studies (mean age in Study I = 10.54, Study II = 11.83, Study III = 8.63).

DD has, in general, been treated as a homogeneous learning disability in which difficulties are believed to be experienced with various aspects of mathematics. Given the disparate screening measures traditionally used and the various hypotheses regarding DD that have been supported in the research literature, we questioned whether the putatively homogeneous population of children with DD is truly homogeneous. Thus, in study II and III, we investigate the possibility that the population of children having “global” problems with mathematics in fact consists of unidentified subpopulations. To this end, in study II, we identified two groups with DD that seemed to exhibit different mathematical difficulties. It is, however, important to note that these subgroups, and the disparate mathematical difficulties they show, are often intermixed and treated as one supposedly homogeneous DD population. One group showed circumscribed problems with retrieving arithmetical facts, whereas the other group had general difficulties with mathematics (i.e., conventional dyscalculia characteristics). If these two groups show similar cognitive deficits in terms of domain-general abilities or number processing abilities, then one could argue that the mathematical difficulties stem from a common origin and hence give credence to the notion that DD is homogeneous in terms of its etiology. However, if these two groups show different patterns of cognitive deficits, as elucidated by the analyses of variance, then these groups do not likely represent the same population. Hence, DD should more accurately be conceived of as being a heterogeneous condition that is characterized by different underlying cognitive deficits.

Assessment of cognitive abilities

Multiple tests tapping various cognitive abilities were administered across the four studies. Some of the tests were primarily used as screening measures, whereas others targeted abilities related to the research questions. These tests, and the abilities they measure, will be briefly described below.

General intelligence

Three of the studies included in this dissertation measured general intelligence (Study I, II, and III). In all instances, it was assessed using Raven's Progressive Matrices set B, C, and D. Only a subset was used to save time. This task provides an index of general intelligence and involves problems containing visual patterns with a piece missing (Raven, 1976) whose solution requires logical reasoning. The task is to select from an array, ranging from six to eight pieces, the correct piece that is missing and completes the visual pattern. Each set includes 12 items for a total of 36 problems. The raw scores were either used as covariates or compared to the norms of age-matched peers.

Reading ability

The teachers with whom we were in contact were asked beforehand to exclude children who either received special instructions in reading and writing or were believed to be in need of such interventional resources. Nonetheless, we assessed their reading ability to obtain an additional control. The test took the form of a fairy-tale, and scattered throughout the text missing words were replaced by a blank space (Malmqvist, 1977). There were four alternative words, inside brackets, located beside the blank space that could be inserted in the blank space. Once the children arrived at such a blank space, they had to select which word inside the brackets made the most sense to complete the sentence and the narrative of the story. The test contains 20 test items in all, and the children had to solve as many as possible during 4 minutes.

Mathematical ability

Mathematical ability was used as a screening measure. Children with DD had to perform below a certain percentile to be included in a DD group. The mathematical tests were timed and consisted of either a) written multidigit calculations (e.g., 57+42), b) fact retrieval problems that had to be solved within 3000 ms (e.g., 5+3), c) arithmetic equations (e.g., 3 + _ = 5), or d) arithmetic fluency tasks that involved solving as many simple calculation problems as possible (e.g., 6-2) within the allotted time. Performance on these mathematical tests was compared to either a control group of typically achieving peers (study I and II) or a norm group (study III).

Visuospatial working memory

A visual matrix task was used to measure visuospatial WM. A visually presented matrix of squares, initially 3 x 3, appeared on a computer screen. In one of those squares there were two black dots, and the participant had to decide whether they were of equal size and to press one of two corresponding keys on a keyboard. Next, a second pair of dots appeared in another square of the matrix, while the former pair was still visible, and the participant once again had to decide whether the new pair of dots was of equal size. Depending on the difficulty level, additional pairs of dots appeared on the screen. After a predetermined set of dots had been presented, the matrix disappeared from the screen. Next, the participant was given a piece of paper with the exact same matrix depicted without of any dots. The task was to recall in which squares of the matrix the dots appeared and mark them down on the paper. The initial matrix had 3 x 3 squares in which two pair of dots appeared representing a working memory span of two items if correctly recalled. The next level contained a matrix of 3 x 4 squares in which three pairs of dots appeared. In this manner, the task became increasingly more difficult, with the hardest level involving a matrix of 6 x 5 squares with seven pairs of dots. Each difficulty level consisted of two trials. The number of correctly recalled pairs while answering size judgement correctly yielded an index of visuospatial WM ability.

Verbal working memory

A listening span task (Daneman & Carpenter, 1980) was used to assess verbal WM. The participant was orally presented with sequences of three-word sentences and the participant is instructed to determine whether the sentence made sense or was syntactically or semantically absurd. If it made sense, the participant orally answered “yes”; if it did not, the participant answered “no”. At the same time, the participant was asked to remember the first word of the sentence. After a given number of sentences had been read out loud, the participant was asked to recall all of the words, in the correct order, that were located first in each sentence. Initially, two sentences were read out loud, which required the participants to recall two words, corresponding to a verbal WM span of two items. The number of sentences increased incrementally by one sentence at a time, with two trials per span size, making each level successively more difficult. Thus, the next span level contained three sentences, the next after that contained four sentences, and so on. The number of words correctly recalled in order was used as a measure of verbal WM.

Executive functions – shifting and inhibition

The ability to effectively shift between tasks and procedures is one executive function, together with inhibition and updating (Miyake et al., 2000). Shifting was assessed using a Trail Making Test (McLean & Hitch, 1999; Reitan, 1958; van der Sluis et al., 2004) composed of two conditions. The first condition (A) contained 22 circles, in which each circle contained a printed digit, and the second condition (B) also contained 22 circles, but with either a digit or a letter printed inside. In condition A, the task was to draw a line, as fast as possible, between the circles, thereby connecting them, in ascending order. In condition B, the participants were instructed to connect the circles as quickly as they could in ascending order once again, but now alternating between letters and numbers (1-A-2-B-3-C etc.). The shifting ability was assessed by subtracting the completion time, in seconds, for condition A from that for condition B.

Inhibition was measured using a Stroop task, in which the stimuli consisted of 30 color words (red, green, blue etc.) whose meaning was incongruent with the ink colors in which they were printed. The task was to name aloud as quickly as possible the ink color in which each word was printed while ignoring the semantic meaning of the word. A measure of inhibitory control was obtained by subtracting the mean response time for the color naming task, described below, from the total response time for the Stroop task.

Lexical speed

The color naming task is a type of Rapid Automatized Naming task (RAN; Denckla & Rudel, 1976), and it is used to control for lexical speed of access to information in long term memory. It is mainly used as a control task because it involves behavioral responses involved in other numerical tasks, such as digit naming. Performance on this task is also used as a measure of general speed and used in ANCOVAs to control for cognitive speed in number processing tasks on which speed is of the essence. The test was administered on two separate sheets of A4 paper, where strings of "XXX" were printed in different colors (red, green, blue etc.) in two separate columns for a total of 30 strings. The participant was instructed to name the color in which the strings were printed as quickly as possible without making any errors. The response times for the two sheets of paper were used as a measure of speed of access to semantic information in long-term memory (Temple & Sherwood, 2002).

Symbolic number processing

A digit comparison task was used to measure participants' processing of symbolic numbers and access to the underlying magnitudes. Two Arabic numerals were simultaneously and horizontally displayed on a computer screen. The objective in this task was to decide which of the two numerals was the numerically larger one and to respond by pressing "A" to indicate the left numeral or "*" to indicate the right numeral. The numerals were visible until the participant pressed a button. Two numerical distances were used: 1 (e.g., 2-3) and 4-5 (e.g., 4-9, 3-7), across a total of 32 trials. Both the response times and accuracies were recorded as measures.

Digit naming is a task that requires the participant to name printed numerals as quickly as possible. Two sheets of paper were used in this experiment, and in the one-digit condition, there were seven rows of the numerals 1-9. Each numeral appeared once in every row, resulting in 63 numerals in total. The two-digit condition consisted of six rows and 27 numerals, and each numeral appeared twice. The participant was told to name each numeral as fast as possible without making any errors. The mean response time that it took for the participant to name all of the numerals was used as the dependent measure.

Number line estimation

This estimation task measures the linearity of the participant's symbolic mental number line, which rests on the ANS and the mapping between the number line and the ANS (LeFevre et al., 2010; Piazza, 2010; Siegler & Opfer, 2003; von Aster & Shalev, 2007). Participants had to indicate with a pencil where a particular number would go on a 0 to 1,000 number line, similar to the procedure used by Landerl et al. (2009). Each child received 16 such numbers to plot on the number line. The accuracy of estimates in relation to a perfect linear function (i.e., absolute error) was used as the dependent measure.

Non-symbolic number processing

Individual ANS acuity was measured using a number discrimination task (Halberda et al., 2008). The participants were presented with two intermixed arrays of blue and yellow dots for 800 ms, after which they were asked to determine which color was more numerous and press a color-coded key on the computer keyboard. This task was identical to that used in Halberda et al. (2008), except for the exposure time of the stimulus presentation. Stimulus presentation time was extended to suit younger children and was adapted from Halberda and Feigenson (2008). The task contained 75 test trials. The arrays contained between 5 and 16 dots, and the ratio of colors varied among four ratio bins (1:2, 3:4, 5:6, and 7:8). The acuity of the ANS was computed and fit using a psychophysics model, yielding a Weber fraction (*w*) for each participant (cf. Halberda & Feigenson, 2008). In the fMRI experiment (study IV), this task was modified to accommodate and mirror the sequential stimuli presentation of the time discrimination task. Dot stimuli were taken from the Panamath software (v. 1.21) developed by Halberda and Feigenson (2008) and contained separate arrays of blue and yellow dots rather than intermixed arrays.

Subitizing and enumeration ability were measured using arrays of randomly arranged dots displayed on a computer screen. Participants had to identify and respond orally to the number of dots present as fast as possible. The dots varied in quantity between 1 and 8, and the software recorded response times as the dependent measure. After the participant responded, the screen went blank for 1000 ms, and then, a subsequent trial ensued. Throughout the experiment, the experimenter registered any errors made. Each set of dots, ranging in number from 1 to 8, was presented three times, and there were 24 trials total. Trials with 1–3 dots were used as an estimate of the subitizing speed, and trials with 5–8 dots were used as a measure of the enumeration ability.

Spatial processing

Spatial ability was measured using three tasks across different studies. A mental rotation task was used in study I and III, a paper folding task was used in study I, and a line length discrimination task was used in study IV. The mental rotation task was a pencil-and-paper test identical to the one used in Neuburger, Jansen, Heil, and Quaiser-Pohl (2011), which in turn is based on a test originally created by Vandenberg and Kuse (1978). The test contained two subtests with different stimuli. The first subset contained alphabetic letters and the second consisted of cube figures adapted from Shepard and Metzler (1971). Each subtest contained 16 items, in which the reference was located on the left side and four comparison stimuli located on the right side adjacent to the target. The comparison stimuli always consisted of two correct and two mirrored items. The task was to identify the two matching items, which required a mental rotation, and to respond by marking them with a pen. All of the comparison stimuli were rotated only in the picture plane and in one of six rotation angles.

The paper folding task, adapted from Ang and Lee (2008), is a spatial visualization task containing 20 items. Each item involved the visual presentation of a square piece of paper being folded a given number of times followed by a hole being punched through the paper that pierced all of the layers of the paper. The task was to imagine how this piece of paper would look when unfolded again. Beneath the folded paper, participants were given five alternatives, one of which was correct. Participants marked their answer with a pencil and had 10 minutes to complete the test.

The line length discrimination task is a spatial task adapted from Fias et al. (2003) and Agrillo et al. (2013). Each trial consisted of one reference stimulus, a yellow line, that was presented on the screen for 600 ms. A blue line appeared on the screen after an interstimulus interval of 500 ms. The participants had to estimate which line was longer. Each stimulus pair across 64 trials corresponded to one of the ratio bins 3:4, 4:5, 5:6, and 7:8.

Temporal processing

A prospective time discrimination task measured the time perception ability of the participants. The participant was presented with a reference stimulus centered on the screen in the form of colored ball. The reference stimulus presentation lasted for 3000 ms, followed by a blank screen for 500 ms, after which a target stimulus (another colored ball) appeared centered on the screen. The task was to estimate which of the two stimuli was presented the longest. The reference was always presented for 3000 ms (in study I and III) and always before the target, but the target stimuli duration ranged from 1500 ms to 6000 ms, spanning the range of interval timing (Buhusi & Meck, 2005). Input was provided using a color coded key on a keyboard. This two-interval discrimination paradigm is similar to that used in Cappelletti et al. (2011), but uses a longer stimulus duration. The ratios between the reference and the targets were such that they corresponded to the Weber fractions consistently found in other magnitude dimensions (e.g., Halberda & Feigenson, 2008). The four ratio bins were 1:2, 3:4, 4:5, and 5:6 across 60 test trials, and each participant’s w could be determined by fitting a psychophysical model to the data. In study IV, the stimulus duration was shortened to reduce the amount of time spent in the fMRI scanner, and the task also contained an additional ratio bin (7:8) to allow assessment of adults across 64 trials.

Study I. Development of magnitude processing in children with developmental dyscalculia: space, time, and number

Aim

The primary objective was to enhance our understanding of the etiology and developmental trajectory of number processing in DD by investigating and contrasting competing hypotheses. Specifically, we were interested in resolving whether a non-symbolic number processing deficit precedes, or is preceded by, an impoverished understanding of symbolic numbers. To this end, we administered tasks requiring symbolic number processing, non-symbolic and exact number processing and processing that taps into the ANS. We also wanted to investigate whether the ANS is a specialized system that is exclusively dedicated to numerical quantities or is part of a general system (i.e., ATOM) for approximating magnitudes across several dimensions, such as space, time and other continua. A secondary purpose of this study was therefore to investigate the nature of this shared magnitude system. Our hypothesis was that if children with DD show impairment on tasks tapping into the ANS and if the ATOM model is correct, children with DD should display impaired performance on other tasks pertaining to other dimensions of analogue processing, such as time and space.

Method

The participants were 82 Swedish schoolchildren enrolled in the fourth grade (N = 51) and second grade (N= 31). They were divided into three groups: children with DD enrolled in their 4th year (mean age = 10.52, SD = 0.46), a control group of children with mathematical ability typical of 4th year students (TA4) with a mean age of 10.54 (SD = 0.38), and an ability-matched control group of typical second graders (TA2) with a mean age of 8.79 (SD = 0.29). The TA2 group was primarily used to yield insight into the developmental trajectory of number processing skills. To be included in the DD group, a child had to receive a special education in mathematics and mathematics only. The child had to perform at or below 1.5 SD

from the mean on the mathematics screening test battery. We developed a novel time discrimination task that targeted the interval timing scale (i.e., suprasecond interval), hypothetically eliciting activation patterns in and around the IPS, which is also implicated in number processing (Kaufmann et al., 2011) and spatial processing tasks, such as mental rotation (Kucian et al., 2007). Number processing in DD was investigated using a non-symbolic number discrimination task, a digit comparison task, and a dot-counting task. Spatial processing was investigated using a traditional mental rotation task together with a paper-folding task.

Results and discussion

The initial analyses of domain-general cognitive abilities indicated that the children in the DD group showed intact working-memory performance, both in terms of visuospatial processing and verbal processing. However, they were slower than TA4 on a RAN task requiring quick lexical access to stored facts in memory. With respect to number processing, we found that symbolic number processing was intact in the DD group, whereas performance on the ANS task was not. Interestingly, the calculated Weber fraction, an index of ANS acuity, was significantly different even when compared to the younger control group of second graders (w = .89 in DD versus w = .26 in TA4 and w = .49 in TA2). In addition, the DD group did not show impaired accuracy or a slower performance on exact non-symbolic processing (i.e., subitzing and enumeration). Taken together, this lends support to the hypothesis that DD is due to a deficit in the ANS that is prior to any deficit in symbolic number processing. This runs contrary to the suggestion made by Noël and Rousselle (2007) that an ANS deficit manifest in children is the result rather than the cause of deficient symbolic number processing. Our findings favor the view that impaired ANS acuity hampers the acquisition and mapping of number symbols, which, in turn, leads to challenges in attaining mathematical competency. Observing the results from other magnitude tasks reveal that children in the DD-group not only showed impaired analogue number processing but also impaired temporal and spatial processing. Although the deficit on these measures was not as pronounced as the ANS deficit, where the DD group showed a significantly worse performance than both the TA4 and the TA2 group, the calculated Weber fractions on the temporal task were worse for the DD group than the TA4 group and trended towards being worse than the TA2 group. Performance on the spatial tasks (i.e., mental rotation and paper folding) was also lower for the DD group than the TA4 group even when controlling for non-verbal intelligence. Feigenson (2007) reasoned that if different magnitude representations share a common mechanism, deficits in one dimension should be paralleled by deficits in other magnitude processing abilities as well. A conclusion of this study is that because all of the dimensions are implicated in DD, Feigenson’s (2007) hypothesis is supported, and those dimensions share representational mechanisms consistent with the ATOM account.

Study II. Number Processing and Heterogeneity of Developmental Dyscalculia: Subtypes with Different Cognitive Profiles and Deficits

Aim

The aim of this study was to investigate whether DD in children with different profiles of mathematical deficits have the same or different underlying cognitive profiles in terms of number processing and cognitive abilities. This would illuminate whether DD truly is a homogeneous learning disability resulting from a core deficit, which has been a widespread view (e.g., Butterworth, 2005; Dehaene, 2011; Feigenson, Dehaene, & Spelke, 2004). We examined children with severe arithmetic fact retrieval deficits but a normal calculation ability, corresponding to a suggested subtype of DD (De Visscher & Noël, 2013), and children with deficits in arithmetic fact retrieval *and* calculation ability, corresponding to the conventional notion of DD. These two subgroups were compared with a group consisting of age-matched children with a typical mathematics ability. Given the plethora of hypotheses regarding the etiology of DD and corresponding empirical support for each of these hypotheses, we wanted to explore whether this discrepancy may be because DD, as traditionally conceptualized, constitutes a heterogeneous population of children that perhaps has incorrectly been assumed to be monolithic. This would give insight into whether the etiology of DD is homogeneous irrespective of manifested mathematical difficulties. On the other hand, if they exhibit different number processing deficits, this would indicate that DD may be caused by a variety of underlying causes.

Method

A sample of children (*N* = 77) aged 10-13 years was divided into three separate groups. One group consisted of typical achievers (TA) with the criteria that they received no special instructions in mathematics and performed above the 15th percentile on a battery of mathematics screening tests. The group that displayed circumscribed mathematical deficits on arithmetic fact retrieval (here called *arithmetic facts dyscalculia;* AFD) had to receive special instructions and perform above the 15th percentile on a measure of calculation performance. The group that showed the characteristics of traditional DD, here called *general dyscalculia* (GD), had to display poor performance on all measures (below the 5th percentile). We assessed domain-general cognitive abilities, such as non-verbal intelligence and working-memory abilities, together with a battery of tests tapping various number processing abilities.

Results and discussion

The GD group's significantly slower performance on the non-symbolic discrimination task (even when controlling for IQ, reading and speed of lexical access) provides support for the ANS deficit hypothesis. This finding is consistent with earlier work on DD (cf. Mazzocco et al., 2011; Piazza et al., 2010; Price et al., 2007). They also showed poorer performance on digit comparison tasks even when controlling for IQ, reading speed and digit naming speed, which would control for the influence of the symbolic number system. In addition, children in the GD group showed a larger problem size effect than children in the TA group, indicating that they have noisier number representations subserved by the ANS. In this study, a number line estimation task was administered, which is believed to tap into several abilities, including the ANS, the symbolic system and spatial abilities, which together are responsible for the mapping process and the subsequent formation of the mental number line (von Aster & Shalev, 2007). The GD group showed an impaired number line estimation skill, even when controlling for symbolic number performance, which suggests that the underlying ANS representations are noisier than their typically achieving peers'. The most parsimonious interpretation is that the GD group suffers from a primary deficit in the ANS, likely subserved by the IPS in the parietal cortex. This dysfunction may then cascade into other areas of number processing, such as symbols, and hamper the acquisition of an accurate and linear symbolic number system.

The AFD group, on the other hand, showed a cognitive profile unlike that of the GD group. ANS acuity seemed intact, as reflected by their scores on the non-symbolic discrimination task, but they showed poorer performance on the symbolic number comparison task. Additionally, they initially performed worse than the TA group on the number line estimation task. However, when including symbolic number comparison performance as a covariate, thus isolating the effect of the ANS aspect of this task, they performed on par with the TA group. Therefore, the poorer performance on the number line task can be attributed to a compromised symbolic number ability that in turn undermines the connection between symbolic numbers and magnitude representations (e.g., De Smedt & Gilmore, 2011; Noël & Rousselle, 2011). Taken together, these findings favor the access deficit hypothesis in this subgroup of children. A tentative interpretation is that a neurocognitive deficit or underdeveloped circuitry originating in the parietal circuit connecting the IPS and angular gyrus defines this subgroup of children with DD.

An important finding is that we have identified different subgroups of children with DD, each with their own cognitive profile. This emphasizes the need for careful deliberation when choosing selection criteria to identify children with DD to ensure that different subtypes of DD are not conflated, thereby obscuring the genuine underlying pathophysiologies. It is noteworthy that the children in both our DD groups would be fused together into a supposedly homogeneous DD group in other studies (e.g., Landerl, Bevan, & Butterworth, 2004; Mussolin, Mejias and Noël, 2010), which would have obscured the divergent etiologies hidden within that group.

Study III. Heterogeneity of developmental dyscalculia: cases with different deficit profiles

Aim

The aim of the study was to expand our knowledge about DD and to specifically focus on disentangling the potential degree of heterogeneity of the learning disability. In previous research, we established that difficulties in different aspects of mathematics could be derived from different underlying number processing deficits. In this study, we examined whether children with *similar* mathematical deficits all exhibited the same cognitive profile in terms of number processing skills and domain-general cognitive abilities. Research suggests that DD is heterogeneous and that the observed phenotypes might be caused by a multitude of underlying neurocognitive causal factors (Kaufmann et al., 2013; Rubinsten & Henik, 2009) even though DD may seem homogeneous at the behavioral level. Thus, researchers have suggested a distinction between primary and secondary DD (Kaufmann et al., 2013). Group level analyses are imperative to evaluate differences between populations and establish generalizable results, but in this study, we wanted to assess whether previous findings from group studies are applicable at an individual level. For that purpose, we carried out a case study of four children with DD. The objective was to investigate the four cases' cognitive deficit profiles and to identify whether they pointed toward a single or multiple hypotheses of DD. The latter outcome would suggest that DD may arise from a plurality of underlying causes. Given the results, we also made tentative hypotheses about the neurocognitive underpinnings giving rise to these demonstrated deficits, which would guide future neuroimaging studies.

Method

In this case study, we tested four children (two boys and two girls) on a comprehensive battery of tests. Three of the children were in 2nd grade, and one child was in 3rd grade. To be included in the case study, the children had to receive special instruction in mathematics and in no other subject, while showing no symptoms of other neurodevelopmental disorders, such as ADHD. They also had to perform above the 15th percentile on a subset of Raven's Standard Progressive Matrices (RPM; Raven, 1976), ensuring that general intelligence is within the normal range. The children also had to score within the normal range (i.e., > 10th percentile) on two reading tasks to exclude comorbidity issues. In addition, the children had to perform below the 10th percentile on each mathematical task that we administered as a screening measure. The percentiles were calculated by comparing the children against four independent norm groups. The data from the norm groups had been independently collected at different points in time, with sample sizes ranging from 53 on some tasks to 303 on other tasks. Children in the norm groups all had Swedish as their native language and normal or corrected-to normal visual acuity. The DD cases and the norm groups were all assessed on a battery of tests tapping both domain-general abilities, such as working memory, executive functions (shifting ability), and lexical speed, and domain-specific tasks pertaining to magnitude and number processing.

Results and discussion

From the collected raw data we calculated individual z-scores for all tasks to determine the degree of normality. Thus, a z-score of 0 indicates a perfectly normal performance (50th percentile), whereas deviating scores, either positive or negative, indicate an individual performance relative to the norm. A z-score of -1.29, below the 10th percentile, was considered to be a substantial deviation from the norm and was subsequently used as a cut-off criterion when classifying a child as impaired on that particular task.

Case 1 (C1) showed impaired performance on all of the magnitude processing tasks, including ANS acuity. C1 also demonstrated a weak visuospatial WM capacity but intact verbal WM and executive functions. One interpretation is that C1 had normal overall WM capacity, but difficulties with encoding and retaining spatial information in working-memory stemming from impoverished spatial information subserved by the IPS. The fronto-parietal network subserving visuospatial working memory includes structures such as the IPS and inferior frontal gyrus (Rotzer et al, 2009). Thus, the IFG may receive compromised data from the IPS via the dorsal visual stream, manifesting itself as impaired visuospatial WM. This cognitive profile suggests primary DD with a magnitude processing subtype. Like C1, Case 2 (C2) showed an impaired magnitude processing ability. However, the impairments were not circumscribed solely to magnitude; working memory capacity, both verbal and visuospatial, was impaired together with executive functions. It is likely that a few key structural connections or cortical loci are dysfunctional in frontal areas, which in turn cascade into large-scale cognitive deficits in number processing as well as domain-general processing. C2 was categorized as having primary DD with combined magnitude and general cognitive difficulties. The profile of Case 3 (C3), by contrast, suggests an access deficit, given the pronounced impairment on the symbolic number processing task and normal ANS acuity, suggesting an impaired mapping of symbols to their underlying quantity representations. However, given the observed deficits in frontally supported abilities, such as visuospatial WM and shifting ability, C3 may have primary DD with conjoint domain-general deficits. Case 4 (C4) did not show any impaired number processing or magnitude processing at all, but did perform poorly on verbal WM and shifting tasks. Thus, the mathematical difficulties are likely soley caused by a domain-general cognitive impairment, a characteristic of secondary DD.

A conclusion is that DD may arise from a plurality of underlying cognitive causes despite the behavioral similarities in terms of the mathematical difficulties that are observed in these children. Another conclusion is that the distinction between primary and secondary DD is difficult to apply, even at an individual level. We also question whether secondary DD must exclude numerical difficulties or whether they can coexist with domain-general impairments.

Study IV. Magnitude processing in the brain: an fMRI study of time, space, and number as a shared cortical system

Aim

The aim of this study was to investigate whether there is a shared cortical system that is responsible for representing magnitudes independent of dimension or whether each dimension of magnitude is represented by domain-specific cortical processes. The ATOM model (Bueti & Walsh, 2009; Walsh, 2003) states that space, time and number are supported by a partly shared general magnitude system but also by dimension-specific processes. This shared magnitude system was initially hypothesized to be located in the right parietal lobe (e.g., Walsh, 2003). However, based on empirical findings, Bueti and Walsh (2009) narrowed the location to the bilateral IPS. Utilizing an fMRI paradigm, we intended with this study to investigate how the brain processes magnitude information across three dimensions – time, space, and number. A whole brain voxel-wise analysis was performed to explore the neurocognitive underpinnings of the processing of these dimensions. It was predicted that the IPS would be a central hub of this system. In line with previous research (Hayashi et al., 2013), we also hypothesized that the IFG would show conjoint activation across dimensions.

Method

A sample of healthy adults (N = 29) was initially recruited; four of them were ultimately excluded due to excessive head motion. During the fMRI session, the participants performed three experimental tasks, each pertaining to a specific magnitude dimension. Each experimental task also had a similar control task that was used a contrast and in which the same stimuli were used and the same decision and motor processing were involved. An alternating block design was used, and each magnitude task consisted of making discriminations between two subsequently presented tasks (see Fig 2). After data acquisition, the preliminary fMRI data analyses consisted of preprocessing steps, including realignment of volumes, coregistration with anatomical images, normalization into MNI space, and smoothing. The general linear model (GLM) in SPM8 (Wellcome Department of Cognitive Neurology, London, UK) was used for statistical analyses of BOLD images, and after a whole brain voxel-wise analysis, we performed a second-level random effects analysis for each magnitude against the contrast. The degree of coactivation across magnitudes was investigated using a conjunction analysis.

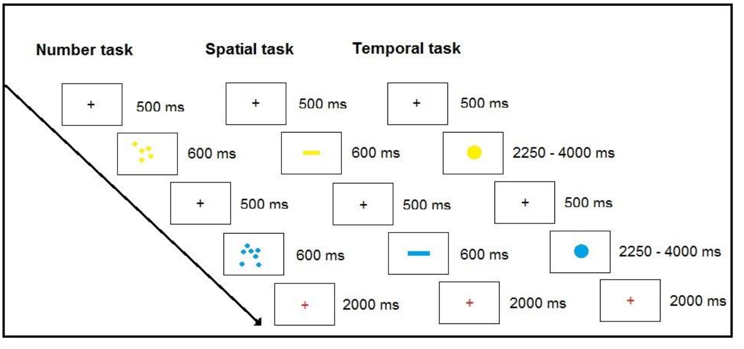

Figure 2. Overview of the task paradigm.

Results and discussion

Significant BOLD activation was found primarily in the right hemisphere (see Fig. 3). Only one structure in the left hemisphere—the insula—was involved in magnitude processing. Significant BOLD activation was found in frontal regions, such as the right IFG, premotor cortex, DLPFC, and insula. In the parietal cortex, activation was restricted to the right SMG and IPS.

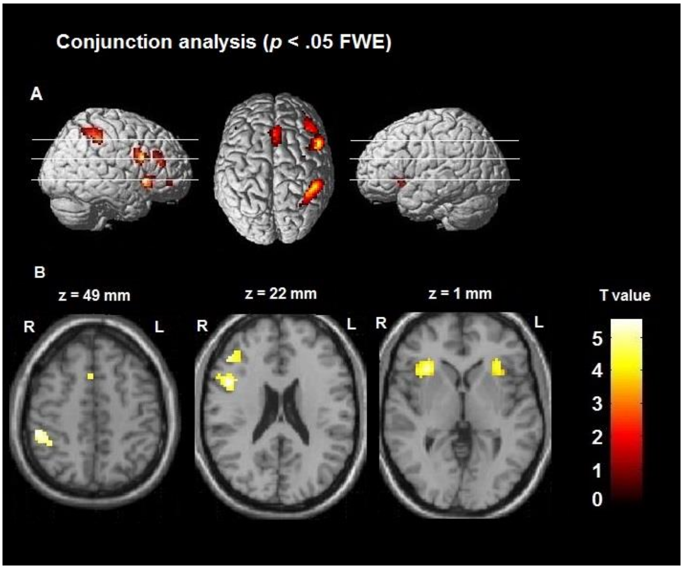

Figure 3. Overlapping neural activations across all of the magnitude processing tasks including a rendition of the overlapping activations in (A) and slices indicating areas of interest in (B).

The results give credence to the notion that the right IPS may play a constitutive role in the magnitude processing system and function as a central hub responsible for the abstract representation of magnitude across dimensions. We also posit that the insula, together with the IPS, is a key node in a magnitude processing system. Uddin et al. (2010) showed structural connectivity in terms of myelinated axon fibers between the insula and the anterior IPS. The insula has been suggested to be part of a salience network that is responsible for identifying stimuli from a continuous stream of sensory stimuli and subsequently marking such stimuli for additional processing (Menon & Uddin, 2010). We suggest that the insula may receive input from topographic representations of magnitude in the IPS and then engage in bottom-up detection and elongated activation to process magnitude as salient units.

General discussion

Despite the fact that DD has been, and continues to be, ill-defined and that its characteristics have been widely disputed across several academic disciplines, there is at least a consensus that there is a group in the bottom 3-7% whose condition deserves attention. Given the plethora of plausible hypotheses put forward by various researchers, my initial stance was quite open-ended when first embarking on this research project: How can we characterize DD? What are the potential causes of DD? Is DD a homogeneous learning disability? What cognitive abilities are important during mathematical problem solving, and what are the neurocognitive processes subserving them? One aim was to identify children with DD and tease out the underlying cognitive abilities and processes that undermine their ability to acquire numerical competency. We specifically investigated whether these children had basic deficits in handling symbolic numbers or whether they showed impaired semantic representations of quantity. In addition, we investigated how domain-general skills possibly relate to this learning disability and whether the ANS is a dedicated system relating to numerosity alone or whether it is better conceived of as being part of a general magnitude system.

The principle findings include that children with DD show markedly reduced abilities to process non-symbolic numerosity and other magnitudes (Study I, II, III) and that numerosity is likely part of a shared magnitude system that includes other dimensions such as time and space (Study I, III, IV). When this research project first started in 2011, the main hypotheses were that DD is a homogeneous learning disability caused by a single core deficit attributable to a neurocognitive dysfunction in and around the IPS. The advent of neuroimaging and the resultant findings of neurocognitive correlates of numerosity processing in the IPS likely fueled the persistence of the “core deficit” hypothesis. I suspect, however, that the community was partly struck by an overly optimistic dose of wishful thinking, insofar as we hoped to, in a reductionistic fashion, distill all of the complexities of a learning disorder to aberrant activity in a single cortical area. My own approach is in no way immune to this neurocentric optimism, and I do believe that mathematical processing can be understood in terms of certain neurocognitive subsystems that enable and restrain individual potential. However, it is clear that numerical cognition relies on widely distributed neural networks that must also be understood in terms of connectivity in and between systems. The complexity of the central nervous system, together with the fact that DD is, more often than not, comorbid with other neuropathologies, such as ADHD and dyslexia (Ashkenazi et al., 2013; Shalev et al., 2000), suggests that one must be sensitive to heterogeneous expressions of mathematical difficulties. Thus, the topic of heterogeneity of DD is central to the findings of two of our studies (Study II, III), in which we highlight that investigations must be targeted at all levels of analyses (i.e., neural, cognitive, behavioral) to understand DD. Understanding the different aspects and deficits of DD is imperative to design and implement targeted interventions or treatments. The topic of interventions and treatment is where I see a potential cross-fertilization between cognitive neuroscience and education, and researchers have started to contribute to this promising field of "educational neuroscience". The journal called *Trends in Neuroscience and Education* is an example of a catalyst for this enterprise. Nevertheless, each of the above points and conclusions from our studies warrant some elaboration.

Magnitudes and symbols - their relation to DD

One central issue in mathematical cognition is the relationship between symbolic representations (i.e., Arabic numerals) and their underlying semantic content. The predominant view stipulates that the innate number sense (i.e., ANS) is an evolutionarily ancient capacity that is phylogenetically shared with other species and that this system is a prerequisite for developing a symbolic system. Moreover, it is widely believed that these two systems are somehow linked and that this mapping processes is initiated as soon as children learn to manipulate number words. Nevertheless, with respect to DD researchers disagree about which of these two systems is the root "cause" of the empirically established deficit. Thus, some have argued that poor ANS acuity hampers acquisition of numerals due to poor semantic mapping (e.g., Mazzocco et al., 2011), whereas others advocate the view that poor symbolic abilities undermine the refinement of the ANS that is evident in normal children (Rousselle & Noël, 2011). The latter would predict that children with DD show slower ANS acuity sharpening throughout development and that processing of Arabic numerals is poor from the onset. When we started our research, there was abundant empirical support for both of these views, and the primary purpose of study I was to shed light on this issue. Children with DD showed a noisier ANS acuity (*w* = .89) than their peers in 4th grade (*w* = .26), while still displaying intact symbolic number processing skills. In addition, we used a control group of children in 2nd grade that were ability matched, to elucidate the severity of the deficit and the developmental trajectory of the number processing systems. The children with DD performed as well as the children in 2nd grade on all number processing tasks, except for the task that measures ANS acuity (*w* = .49 for children in their second year of schooling). They did not show more errors or longer response times. Thus, the most parsimonious interpretation is that an ANS deficit precedes any purported symbolic deficit and that this factor subsequently affects mathematics competency in line with previous suggestions (Feigenson et al., 2013). The role of ANS acuity is highlighted in research by Libertus and Brannon (2010), in which infants who made finer nonsymbolic number discriminations at 6 months also showed superior and sharper ANS acuity 3 months later. In addition, Mazzocco et al. (2011) found that ANS acuity at age 3 or 4 years predicts standardized math scores at ages 5 and 6, thereby showing an association between ANS acuity and math proficiency prior to formal math instruction. Together, these findings emphasize the importance of the ANS in acquiring mathematical skills. However, it is plausible that the ANS and cultural exposure to mathematical symbols have a bidirectional relationship. Geary (2013) suggested that ANS acuity is driven both by the maturation of brain systems as well as culture and experience. Recent research has shown that experience with mathematical material likely sharpens and calibrates the ANS (Lindskog, Winman, & Juslin, 2014; Nys et al., 2013). Therefore, it is plausible that ANS acuity and mathematical experience have a bidirectional relationship, but our studies suggest that an ANS deficit most likely precedes symbolic number processing impairments and subsequent mathematical difficulties in a certain population of children. In another study, we performed multiple regression analyses on 133 school children to determine whether symbolic and non-symbolic number processing would predict mathematical abilities. The results revealed that ANS acuity did not predict mathematical abilities, whereas symbolic number processing did (Skagerlund & Träff, 2016). This supports the notion that children with DD show atypical ANS acuity that hampers the acquisition of mathematical abilities and that the population of children at the lowest end of the spectrum represents a qualitatively different population whose difficulties with mathematics are not graded along a continuum. Children above this segment of the population, regardless of whether they can be classified as low achievers or typical achievers, demonstrate an ANS acuity that does not substantially contribute to mathematics outcomes. This mirrors the findings and conclusions of Mazzocco et al. (2011) that children with DD constitute a different population than children with poor performance of math (i.e., low achievers) and that the ANS is an important factor implicated in DD. This is echoed in the data from study II, in which we identified a group of children with general difficulties with mathematics, corresponding to the traditional conceptualization of DD, who showed pervasive impairments on tasks taxing the ANS. The case study (Study III) revealed that one child, C1, also fit this category of children with a cognitive profile suggestive of an ANS deficit. In addition, children with an apparent ANS deficit did not exhibit a circumscribed impairment limited to judgements about numerosity but a broad impairment that encompassed judgements about magnitudes in general.

Number processing as magnitude processing

Previous research has suggested that time, space, and number share neurocognitive correlates in the human brain (e.g., Bueti & Walsh, 2009; Walsh, 2003) and this hypothesis is supported by behavioral interference paradigms (cf. Bonato et al., 2012; Fabbri et al., 2012). This led Feigenson (2007) to suggest that if diverse magnitude representations share a common mechanism, deficits in one dimension should also be accompanied by deficits in other magnitude dimensions. This suggestion, together with the fact that children with DD consistently display problems with numerosity, fueled our hypothesis that children with DD may have an amodal magnitude processing deficit rather than an isolated difficulty with the apprehension and manipulation of approximate numerosities. Findings from our studies (Study I, III, and IV) led us to conclude that (1) there is a general magnitude processing system and that (2) this system is implicated in a population of children with DD. The results from study I indicate that children with DD have a deficit in a magnitude system, which affects their ability to perform as well as their peers on tasks pertaining to space, time, and number and in turn impairs their ability to engage in—and learn—mathematics. Corroborating these findings, the data from study III indicates that children with an ANS deficit also showed parallel deficits in processing other magnitudes. More succinctly, if a child demonstrated any performance decrement on any magnitude processing task, their performance was poor across the board on all dimensions. These studies alone, however, do not allow any substantial claims to be made about the structure or neurocognitive mechanisms subserving this system. Thus, we conducted study IV to explore this matter using neuroimaging. Neural activity patterns were identified in a predominantly right lateralized system, which included the right IPS, right premotor cortex, and bilateral insula (see Fig 4). Conjoint activations were also evident in right IFG and frontal eye-fields, which were interpreted as being part of categorical decision-based representations of the magnitudes provided through the dorsal visual stream. We suggest that the right IPS represents cardinal properties of magnitude and that the insula involves salience detection and awareness of magnitude in a generalized magnitude system. This functional coupling is supported by the established structural connectivity between the insula and the anterior IPS (Uddin et al., 2010). Uddin and colleagues (2010) proposed that the IPS receives information from visual cortices, which is then projected to the anterior insula via the superior longitudinal fasciculus. Thus, magnitude units, irrespective of dimension, are initially marked as salient by the anterior insula after receiving input from topographic representations of magnitude in the IPS (Harvey et al., 2013). This highlights the intricate relationship between attention and magnitude representations, insofar as the insula may be involved in bottom-up detection and elongated activation to process magnitudes, such as numerosity, as salient units.

The magnitude system may be dysfunctional in children with DD, which results in a "hypergranularity" of mental representations of magnitude that impedes the higher order cognitive abilities that are reliant on these magnitudes. A similar account has been provided by Simon (2008) in children with 22q11.2 deletion syndrome, a genetic disorder resulting in complex cognitive dysfunctions pertaining to visuospatial abilities, temporal abilities, and numerical abilities. The impoverished magnitude acuity (or hypergranularity) in DD may result in inefficient mapping of numbers onto the spatiotemporally based number line. The magnitude processing deficit in DD can likely be traced to aberrant functioning of the IPS, but our study does not allow for more specific analyses of any potential functional subdivision of the IPS. Uddin et al. (2010) used structural and functional connectivity analyses and found evidence of three subdivisions of the IPS, each with their own profile of neural network connectivity. For example, the posterior IPS (hIP3) was more connected to visual cortices. One of the two anterior parts of the IPS (hIP2) had projections to frontal cortices via the dorsal visual stream in a fronto-parietal network, and the anterior-most portion (hIP1) connected to the inferior frontal cortex and insula. These findings led the authors to suggest that these subdivisions and networks have slightly different functional roles in mathematical processing. The posterior part of the IPS may be more involved in decoding visual information into semantic and spatial representations of quantity, while the anterior IPS may subserve complex mathematical operations reliant on fronto-parietal circuits. Thus, the affected magnitude processing acuity observed in DD may be a result of multiple loci in the magnitude processing network; hypothetically, specific subdivisions of the IPS may be dysfunctional, resulting in slightly different neuropathologies of magnitude processing, or the insula may inhibit effective salience processing of magnitude. Future studies using high field fMRI, as per Harvey et al. (2013), and functional and structural connectivity analyses, as per Rykhlevskaia et al. (2009), could potentially disentangle the different roles of these nodes in the magnitude processing network and the intimate relationship between perceptual processes reliant on occipito-parietal networks and attentional processes reliant on fronto-parietal connections.

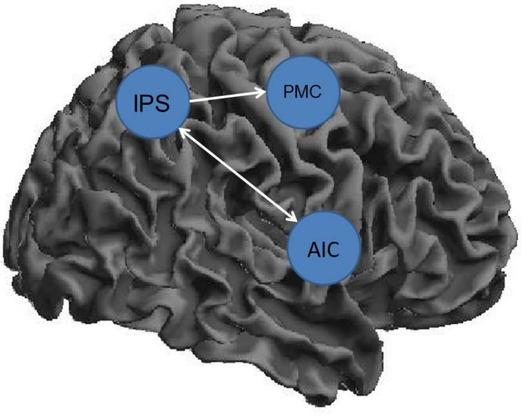

Figure 4. Schematic diagram of the suggested core components of the generalized magnitude system. The IPS decodes information from the sensory cortices and projects information to the anterior insular cortex, where magnitude representations are coded for saliency or acuity and sent back to the IPS. This information is then projected to the premotor cortex to code for action, in line with Walsh (2003).

Despite the absence of detailed specifications and characteristics of this magnitude processing system, the goal of our study (Study IV) was to establish that there is indeed a magnitude processing system pertaining to magnitudes irrespective of dimension. By administering three different magnitude tasks, we provide support for the notion that numerosity processing is part of a generalized magnitude processing system and that this system is likely implicated in a population of children with DD. However, together with our other studies, it became evident that this group of children with mathematical difficulties was not alone. The data suggest that children with DD can be differentiated into subtypes, each with their own cognitive profile that undermines the acquisition of mathematical competency.

Heterogeneity of DD – subtypes with specific cognitive profiles

Despite the general belief that DD may be reducible to a single core dysfunction in the brain, researchers have acknowledged the behavioral disparities in children with mathematical difficulties (e.g., Geary, 2004). Indeed, our data in study II suggests that children may have difficulties with different aspects of mathematics (i.e., general problems with mathematics vs.

circumscribed problems with access to arithmetic facts), which we hypothesized could be due to different underlying cognitive deficits. Indeed, our findings indicated that children in a putatively homogeneous population could actually be characterized as having mathematical difficulties as a result of two different cognitive weaknesses. One group of children showed global difficulties with calculation and access to arithmetic facts, which we found could be attributed to deficits in the ANS. By contrast, the other group of children (in that paper referred to as *arithmetic facts dyscalculia*), whose weakness was limited to rapid access to arithmetic facts, demonstrated an intact ANS in combination with a markedly impaired performance on symbolic number tasks. Thus, the hitherto puzzling empirical situation in research on DD, in which researchers have advocated seemingly competing and incompatible hypotheses, may be resolved if the heterogeneity of DD is acknowledged and further investigated. This was the target of investigation in study III. Prior to this study, it was reasonable to assume that difficulties with different mathematical aspects may be caused by different underlying cognitive profiles and deficits. Nevertheless, we wanted to further explore the heterogeneity of DD by investigating whether children with *similar* difficulties with mathematics could be differentiated in terms of their underlying cause. Four children were identified as having severe, but similar, difficulties in learning mathematics. Around this time, several researchers congregated and urged that primary and secondary DD be distinguished to emphasize the heterogeneity in children's difficulties (Kaufmann et al., 2013; Price & Ansari, 2013). Kaufmann et al. (2013) proposed that secondary DD should be used if "*numerical/arithmetic dysfunctions are entirely caused by non-numerical impairments (e.g., attention disorders)*" (p. 4), whereas primary DD roughly corresponds to the traditional notion of DD and is defined as a "…*heterogeneous disorder resulting from individual deficits in numerical or arithmetic functioning at behavioral, cognitive/neuropsychological and neuronal levels"* (p. 4). These definitions are sound and may prove useful in communcation among resarchers, teachers, and clinicians. Therefore, our objective was to apply this distinction in our case study, which proved challenging even at an individual level.

The advantage of administering a comprehensive test battery to a single individual is that it allows the identification of relative strengths and weaknesses. In this vein, performance on any given test and its construct can be understood in the context of performance on other tests. It is rare to find tests that are "pure" in their measurement of the ability in question, in the sense that they are not contaminated by other unintended cognitive processes. One established example is working memory tasks, which also require effortful attention and involvement of executive functions (e.g., Rudkin, Pearson, & Logie, 2007). Thus, the administration of a test battery tapping several cognitive abilities enabled us to create a nuanced cognitive profile of each child. For example, C3 displayed a profile suggestive of an access deficit. However, given the coexisting deficits in executive functions and visuospatial working-memory, it cannot be ruled out that these deficits play a causal role in the apparent number processing deficit. Performance on the symbolic number comparison task may have been affected by executive functions. Another possibility is that poor executive functions may have impeded the mapping of the symbols over the course of development. However, by recognizing that this child has a normal reading skill, which involves symbols and their semantic referents, and performs normally on the ANS task, we can plausibly conclude that this child has a specific deficit in number processing involving symbols. Irrespective of the actual neurocognitive causal chain that gives rise to the apparent profile of C3, the ambiguity of the data strikes at the heart of the debate about the etiology and distinction of primary and secondary DD. According to the definition of secondary DD, any demonstrated mathematical difficulty can be attributed *entirely* to non-numerical factors. A strict interpretation of primary DD would be that a child has to show *only* number processing deficits while displaying no such deficits in domain-general cognitive abilities. A more lenient interpretation would state that a demonstrated number processing deficit is both a *necessary and sufficient* criterion for primary DD, in which case number processing deficits and domain-general deficits can coexist. Thus, although the distinction between primary and secondary DD is a welcome addition to the discussion of heterogeneity, our results raise the concern that this may nonetheless be too simplistic a distinction to capture the complexity of this learning disorder. One might also question whether secondary DD is a misnomer to begin with. If a child shows perfectly intact number processing abilities, and her mathematical difficulties can be attributed entirely to problems with indirect cognitive abilities (such as attention), is it then fair to say that this child suffers from DD? If this child suffers from ADHD, which in turn affects the learning outcome negatively in mathematics, the term secondary DD is simply inaccurate and confusing. Conversely, if the intended meaning of secondary DD is that a child has circumscribed problems with attaining mathematical competency due to poor attentional skills that are not severe enough for a diagnosis of ADHD, it may be a more accurate label. Nevertheless, there is a risk of obfuscating and diluting our understanding of the etiology of this cognitive profile by associating it with a neurobiological predisposition and risk factor, such as "pure" DD. Thus, the term MLD may be better able to capture the cognitive profile of this population of individuals, as Rubinsten and Henik (2009) have suggested. It is absolutely imperative that our delineations and definitions of neuropathologies are as succinct and accurate as possible if we are to provide effective interventions and treatments.

Taken together, the data from our four studies suggest the following, admittedly preliminary, non-comorbid subtypes of DD:

Primary DD subtypes

a) Magnitude processing subtype
b) Access deficit subtype

Secondary/MLD subtype

c) Executive and working memory subtype

Complex DD subtype

d) Primary + Secondary DD

These subtypes of DD are most likely caused by distinct neurocognitive dysfunctions across distributed neural systems, and these subtypes may in some cases be comorbid with ADHD or dyslexia. Effective educational interventions, which are primarily implemented at the behavioral level in school environments, are informed and constrained by behavior and cognition at a higher level of abstraction than neurocognitive processes. However, if we can understand the neurocognitive networks involved in the various subtypes of DD, we should be able to leverage this knowledge and inform our understanding of plausible mechanisms by which interventions may work. Thus, below is a brief outline of the possible dysfunctional neurocognitive networks involved.

Candidate neurocognitive correlates of DD

As described earlier, the magnitude processing subtype of DD may involve aberrant magnitude processing subserved by a distributed network partially relying on occipitoparietal visual processing. The posterior IPS has structural connections with extrastriate visual areas (Uddin et al., 2010), indicating that this cortical circuitry may be susceptible to abnormalities. They could subsequently interfere with visuospatial processing. Uddin et al. (2010) suggested that the posterior IPS may play a role in transforming symbolic and non-symbolic numerical information to spatial and semantic representations of quantity. Additionally, the anterior IPS has structural connections with the insula (Uddin et al., 2010), which we also found to be part of a network for general magnitude processing (Study IV). Neurocognitive correlates would likely be traced to the right IPS and the dorsal visual stream.

The access deficit subtype of DD, characterized by ineffective mapping between symbols and the underlying magnitudes, demonstrates a seemingly simple cognitive profile; it is simple insofar as it seemingly, at the surface level, involves one intact ability (i.e., representing the semantics of numerosity) and one dysfunctional ability (i.e., accessing those underlying representations from symbols). Merely glancing at digits, as opposed to glancing at nonsensical symbols, has been shown to elicit activation patterns in the angular gyrus (Price & Ansari, 2011), and Price, Mazzocco and Ansari (2013) found that angular gyrus activity correlated with PSAT math scores in adolescents performing mental arithmetic. Interestingly, right IPS activation was inversely correlated with PSAT scores, which may indicate a functional immaturity of the angular gyrus in individuals less proficient at mathematics. It is therefore tempting to conclude that children with an access deficit subtype of DD have a neurodevelopmental delay in forming robust symbolic representations subserved by the angular gyrus. Although this scenario is plausible, one must be wary of alternative and equally plausible neurocognitive candidates that could give rise to this phenotype. Another source of this access deficit can likely be traced to ineffective hippocampal involvement in forming lasting neocortical memory traces for arithmetic and symbolic facts. Structural connections between the posterior angular gyrus and the hippocampus, in terms of strong axonal fiber density, and functional connections have been identified (Uddin et al., 2010), which may subserve the migration of lasting memory traces. Indeed, Rykhlevskaia et al. (2009) used voxel-based morphometry analysis to investigate neuroanatomical differences between children with DD and typical children and found that the hippocampus had reduced gray matter volume in children with DD. Thus, the access deficit subtype of DD may have origins in dysfunctional neural networks between the hippocampus and the angular gyrus.

Secondary DD, or, more aptly, MLD, is likely characterized by deviant or underdeveloped neurocognitive networks in non-numerical areas and connections in the brain. Children with mathematical difficulties and DD often show a poor visuospatial working memory ability compared to their peers (e.g., Andersson, 2010; Schuchardt, Maehler, & Hasselhorn, 2008), which may be attributed to dysfunctional cortical areas in the frontal lobe, such as the DLPFC or inferior frontal gyrus. Visuospatial working memory tasks elicit activations in the right IPS as well, and if numerosity processing is intact in a child with apparent visuospatial impairments, those impairments may be due to a deviant axonal connection in the dorsal stream connecting IPS and the inferior frontal gyrus. During ontogenetic development, typically developing children show an increased white matter density in the frontal lobes, suggesting a maturation of the fronto-parietal network (Ranpura et al., 2013). However, Ranpura and colleagues (2013) found that children with DD do not display the same increase in white matter volume, indicating a developmental delay that may interfere with effective information processing subserved by the fronto-parietal network. In our case study (Study III), we found that children with DD often show difficulties in shifting ability. This ability involves the salience network (Engström, Landtblom, & Karlsson, 2013; Menon & Uddin, 2010) comprising the anterior cingulate cortex (ACC), insula, and DLPFC. Hence, if a child shows a poor shifting ability but intact working memory capacity, the ACC may be the culprit, whereas if the working memory capacity is poor, the DLPFC may be implicated. It is difficult to unequivocally identify candidate neurocognitive structures implicated in secondary DD/MLD, but the aforementioned nodes provide a sketch of likely sources of deviant neurocognitive processing that cascade into difficulties with mathematics.

Even though it may be discouraging to concede that mathematical difficulties may arise from many different neurocognitive causes, such that the hitherto seemingly homogeneous DD is subject to subtyping into groups, it is my firm belief that we can leverage our knowledge and find behavioral markers of underlying neural deficits. By administering a well-composed battery of tests, as we did in study III, it may be possible to identify and use behavioral performance measures as proxies for underlying neurocognitive patterns. In turn, we can implement targeted interventions that take the cognitive profile of each child into account to isolate and remediate neurocognitive vulnerabilities. This is our next topic.

Educational implications

The connection between cognitive neuroscience and education is presently being established, and because the brain is an organ that is intrinsically involved with learning, there is a natural link between knowledge about how the brain works and education (Ansari, Coch, & De Smedt, 2011). Nevertheless, it is essential that one is humble about the potential transfer and impact of neuroscience, which is concerned with phenomena on the lowest level of abstraction, to educational settings, in which the ultimate performance of any given child is dependent upon so many complex factors that are both endogenous and exogenous to the individual. Cognitive neuroscience will not be able to prescribe a silver bullet to ameliorate every single learning difficulty. However, if important exogenous prerequisites are fulfilled (e.g., a positive home environment and a strong rapport between teacher and learner), findings from cognitive psychology and neuroscience can inform and guide targeted interventions at the individual level. In the long run, cognitive neuroscience and education may form a symmetrical relationship in which both disciplines inform one another about the effectiveness of general educational principles and potential compensatory learning strategies adopted by children (Ansari et al., 2011). The powerful potential for the cross-fertilization of neuroscience and education is exemplified by the findings from Kucian et al. (2011); they created a training regime over five weeks in which healthy children as well as children with DD trained on a mental number line task. Prior to the training period, they scanned each child using fMRI to detect neurocognitive training effects. Kucian et al. (2011) observed training effects on the task, which were expected, and also observed a transfer to mathematical skills. Intriguingly, the training regime also altered brain activation patterns measured in a post-treatment scanning session. Children with DD showed decreased reliance on frontal areas implicated during effortful processing and domain-general abilities as well as increased activation around the IPS five weeks later, suggesting that training potentially ameliorated the previously dysfunctional hypoactive region. These findings indicate that the effects of training resulted in less demands on quantity processing, executive functions and working memory, and that the reduction in activation patterns was more pronounced in the DD group. The children with DD showed the most benefit from the training regime in terms of both behavioural measures and in neurocognitive responses. The work by Kucian et al. (2011) illustrates how neuroscience and education can inform one another and shows promise for future research.

Targeted interventions for different subtypes

Even though an in-depth analysis of different educational interventions is outside the scope of this thesis, some brief pointers may be warranted given that we have identified subtypes of DD; it is likely that different interventional instruments should target different subtypes to maximize their effectiveness. To develop appropriate interventions for children at risk of developing DD, future research should focus on disentangling different cognitive processes when assessing children at risk of developing DD to account for heterogeneity. With respect to the access deficit subtype of DD, Geary (2004) reports that children who struggle with rapid retrieval of arithmetic facts often fail to show improvements throughout the school years. However, these children may benefit from practicing solving arithmetic problems under time constraints that force them to strengthen their memory traces for these facts (Gersten, Jordan, & Flojo, 2005). Such a training regime could potentially help these children by reducing the need to resort to laborious explicit counting strategies (Gersten et al., 2005).

If children cannot retrieve the answer to simple arithmetic facts, they should also be encouraged to use backup strategies, such as relying on known nearby arithmetic facts to compute an answer (an approach known as the *decomposition strategy*).

In contrast to children with an access deficit subtype of DD, children with a magnitude processing deficit may primarily benefit from interventions that promote the development of the mental number line. In fact, promising research indicates that the ANS is malleable and subject to maturation and refinement (DeWind & Brannon, 2012). The authors behind that study found that training on number discrimination tasks improved adults' ANS acuity and numerical precision (DeWind & Brannon, 2012). The natural next step, provided by Park and Brannon (2013; 2014), was to establish that these improvements transferred to adults' mathematics proficiency. By using a set of different training tasks (including a non-numerical short term memory task, a non-symbolic discrimination task, and non-symbolic arithmetic), they could pinpoint the driving force behind training effects (Park & Brannon, 2014). The authors demonstrated that training on a non-symbolic arithmetic task transferred to symbolic arithmetic, whereas a traditional non-symbolic discrimination task did not. Thus, the authors conclude that it is the *manipulation* process that is causally related to the transfer to formal arithmetic. They suggest that children may benefit from training on non-symbolic arithmetic to hone their arithmetical skills before mastering the symbolic system (Park & Brannon, 2014). These results are certainly very promising given that these were adults who showed improvements over time; given the inherent plasticity and malleability of the developing brain, targeted interventions in children are therefore likely to have an even greater long-term impact. However, I believe that one must be careful in generalizing the results from a population of adults, with a presumably fully functional ANS, to a population of children with DD. I suspect that children with a primary deficit in the ANS, which hampers their ability to engage in more complex arithmetic operations, may likely benefit more from basic training to refine their ANS acuity.

Children whose difficulties with mathematics stem from domain-general deficits such as in executive abilities or working memory can engage in a regime that develops these abilities. For example, research has shown that children with ADHD may benefit from working memory training (Klingberg, Forssberg, & Westerberg, 2002) and that these working memory improvements can transfer to other areas, such as mathematics (Holmes, Gathercole, & Dunning, 2009). These findings are, however, controversial insofar as there is a lack of consensus regarding the efficacy of these regimes and their impact on scholastic achievement (Melby-Lervåg & Hulme, 2012). The efficacy of working memory training depends on time-consuming practice, and one might argue that the resources spent on these tasks might be better allocated to the target domain in which the child struggles, such as mathematics. Numerous interventions to aid executive function development have been suggested to be efficacious; in a review, Diamond and Lee (2011) show that a wide array of different interventions (varying from aerobic exercise to playing computer games) can be fruitful as long as they are challenging and continuously increase the demands on executive functions.

Methodological and theoretical considerations

The ultimate purpose of the research project presented in this thesis was to understand the cognitive processes involved in mathematics in general, but in particular, to disentangle what characterizes children with DD. As mentioned in the introduction, this endeavor takes the cognitive underpinnings of the individual as the unit of analysis. Given this research approach, there are some methodological considerations and theoretical issues that should be acknowledged and discussed.

The Brain vs. The Environment

If one advocates the view that cognitive processing is instantiated by neural events in the brain, it becomes easy to become trapped in a reductionist perspective in which cognitive phenomena and development are believed to be primarily driven by endogenous forces. Thus, I think it is appropriate to emphasize that there are both individual forces and sociocultural forces that ultimately shape the developmental trajectory of mathematical abilities. However, I do believe that there is a population of individuals with a specific genotype that are vulnerable to developing DD, given the reported concordance rate for mathematical learning disabilities (70%) in monozygotic twins (Oliver et al., 2004). I also believe that it is possible to identify these children at a young age and to provide various resources to try to ameliorate the weakness in basic magnitude representation. With favorable exogenous factors, such as supportive family relationships and stimulating educational settings, it is possible to avoid full-scale expression and development of this vulnerable genotype. Thus, I favor a view whereby one takes into account the gene-environment interactions that in the end produce the observed phenotype. For example, Caspi et al. (2002) found that children with a polymorphism in the gene that encodes the monoamine oxidase A- (MAOA) metabolizing enzyme were more susceptible to maltreatment during childhood than children without this polymorphism. Children with this polymorphism displayed a greater tendency to develop antisocial behavior later in life. In this vein, the authors argue that children with a specific genotype may be more susceptible to environmental factors (Caspi et al., 2002). A similar finding regarding the risk of developing major depression has been reported (Caspi et al., 2003). The authors identified a polymorphism in the serotonin transporter gene that seemed to render the carriers of this genotype more vulnerable to life stress (Caspi et al., 2003). Wilcke and colleagues (2012) have shown that a polymorphism of the FOXP2 gene is associated with congenital dyslexia. In the same vein, I think that there is a population of children with DD that may have a genetic makeup that makes them vulnerable to developing DD. Nevertheless, it is important to treat these vulnerabilities as risk factors and not full-blown deterministic factors. It does not matter whether a child has a genetic vulnerability with a resultant morphological aberration in the IPS or in white matter integrity. What matters for diagnosis is the final cognitive-behavioral profile and subsequent severe mathematical difficulties that affect the well-being of the individual. To understand the factors and mechanisms involved, we need a multilevel approach consisting of systematic inquiries into the neurocognitive underpinnings of mathematical cognition, gene-environment interactions and top-down investigations of sociocultural and emotional factors that determine the ultimate phenotype.

Methodological considerations

The children classified as having DD in our studies were not formally diagnosed with DD. There is a general practice in this line of research of using standardized mathematics test scores, or other arithmetic tests, and comparing them to norm data to classify children as having DD. In addition, the assessment of mathematical abilities is almost without exception only carried out once. Mazzocco et al. (2011) and Desoete et al. (2012) are laudable exceptions in this respect because they used a criterion of poor performance over time on multiple testing occasions. Thus, there is always the possibility of including false positives in the final sample. However, we tried to minimize this possibility by contacting teachers in special education and asking them to select children with consistent difficulties with mathematics. The use of cut-off criteria in general is in itself controversial, particularly because researchers have used diverse percentile scores to demarcate DD. In fact, a conclusion in studies II and III was the importance of carefully considering appropriate screening measures and percentile cut-offs to ensure that different subtypes of DD are not conflated, thereby obscuring the genuine underlying pathophysiologies. A selection procedure that exclusively relied on an arithmetic fact retrieval task to identify children with "pure" DD, as some researchers have done previously (e.g., Landerl, Bevan, & Butterworth, 2004; Mussolin, Mejias and Noël, 2010), would have mistakenly conflated both GD and AFD into a single heterogeneous sample of children that would have obscured the etiologies within that group. Researchers should also be wary of the percentile used as a cut-off criterion, when the decision will determine the population under scrutiny (cf. Mazzocco et al., 2011). It is important to interpret the current findings in light of the fact that we studied children between 8 to 12 years of age and at a single time point. Therefore, it is crucial that future studies replicate the findings from our fMRI study of magnitude processing in adults to determine whether these findings generalize to children.

Conclusions

The overarching aim of this thesis was to contribute to our understanding of the etiology of DD. Several plausible hypotheses had been proposed, which led to the systematic investigation of each of these, with the ultimate goal of disentangling whether DD truly is a homogeneous disability with a single core deficit that is responsible for its etiology. We also investigated neurocognitive correlates of number processing and other magnitudes that provide the foundation for subsequent mathematical abilities. Our findings lend support to the notion that DD is a heterogeneous learning disability, in which children can be assigned to different subtypes of DD. We identified at least two subtypes of primary DD, which are characterized by specific deficits in number processing, and one subtype that more aptly should be denoted as MLD, whose characteristics include deficits in non-numerical abilities alone. Further research is warranted to potentially identify and delineate additional subtypes in a manner like that of Bartelet and colleagues (2014). Future studies should also investigate the neurocognitive correlates of these subtypes. Our findings also support the hypothesis that numerosity representation is part of a generalized magnitude processing system and that this system is likely implicated in a population of children with DD. Our findings also shed light on the controversy regarding whether non-symbolic numerosity precedes a symbolic processing deficit. Children with one DD subtype show difficulties in representing numerosities that likely hamper the subsequent acquisition of the symbolic system and, ultimately, mathematics.

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