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REVIEW

Developmental dyscalculia

Karin Kucian · Michael von Aster

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Abstract Numerical skills are essential in our everyday life, and impairments in the development of number processing and calculation have a negative impact on schooling and professional careers. Approximately 3 to 6 % of children are affected from specific disorders of numerical understanding (developmental dyscalculia (DD)). Impaired development of number processing skills in these children is characterized by problems in various aspects of numeracy as well as alterations of brain activation and brain structure. Moreover, DD is assumed to be a very heterogeneous disorder putting special challenges to define homogeneous diagnostic criteria. Finally, interdisciplinary perspectives from psychology, neuroscience and education can contribute to the design for interventions, and although results are still sparse, they are promising and have shown positive effects on behaviour as well as brain function.

Conclusion: In the current review, we are going to give an overview about typical and atypical development of numerical abilities at the behavioural and neuronal level. Furthermore, current status and obstacles in the definition and diagnostics of DD are discussed, and finally, relevant points that should be considered to make an intervention as successful as possible are summarized.

Keywords Developmental dyscalculia · Number processing · Calculation · Learning disability · Therapy · Learning

Abbreviations

DD	Developmental dyscalculia
fMRI	Functional magnetic resonance imaging
IPS	Intraparietal sulcus
MRI	Magnetic resonance imaging

Introduction

There is a widespread misunderstanding of the importance of numerical understanding in everyday life and a lack of appreciation of how important math learning is for young children. Numerical abilities are essential in daily routine, and they are becoming even more crucial with the increasing role of technology in contemporary society. Low numeracy skills have a negative impact on the employment prospects and mental and physical health of individuals and on the economic status of countries [37, 72]. Importantly, profound difficulties with numeracy are very common with a prevalence rate between 3 and 6 % [52, 89]. Despite the relatively high occurrence of specific numerical learning disorders, only few research projects focus on this clearly high-priority area. It is important to gain a clear understanding about typical as well as atypical development of numerical competencies on behavioural and neuronal levels to foster the acceptance as a disorder and raise public awareness for the need to provide targeted educational and therapeutic support tailored to affected children.

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K. Kucian (✉) · M. von Aster
Center for MR-Research, University Children's Hospital Zurich, Steinwiesstrasse 75, 8032 Zurich, Switzerland
e-mail: karin.kucian@kispi.uzh.ch

M. von Aster
e-mail: m.aster@drk-kliniken-westend.de

K. Kucian · M. von Aster
Children's Research Center, University Children's Hospital Zurich, Zurich, Switzerland

M. von Aster
Department of Child and Adolescent Psychiatry, DRK-Hospital Westend Berlin and Ernst von Bergmann Hospital Potsdam, Spandauer Damm 130, 14050 Berlin, Germany

In the following sections, we are going to review the typical developmental trajectories of cognitive number representations and contrast these behavioural characteristics to atypical development associated with developmental dyscalculia (DD). In this regard, we are outlining general and critical points that have to be considered in the definition and diagnosis of DD. Since recent findings suggest that DD is a brain-based disorder [e.g. see meta-analysis by Kaufmann [53]], neuronal representations of numbers in the adult and developing brain as well as corresponding neuronal underpinnings of DD are reviewed. Finally, based on current behavioural and neuronal knowledge about DD, a possible intervention method and future outlook are presented.

Ontogenesis and phylogeny of number representations

In our daily life, we are confronted with a huge amount of numbers in various formats—Arabic digits (3), number words (three), Roman numbers (III), time (3 pm), magnitudes (•••), finger signs, words with numeric meaning (triplet, trio), or with ordinal (third) or temporal (e.g. waltz time) information. The expression 'number representation' describes the mental image or construct of such numbers or magnitudes [36]. A challenge during development is to learn to differentiate as well as link these different number representations [13].

Different findings point to the existence of an innate basic number sense that enables even newborns to compare and discriminate between concrete magnitudes approximately [30]. Moreover, a recent study could even demonstrate that foetuses in the last trimester are attentive to numerosity [84]. This basic number system seems to be evolutionary and not only present in humans, but also in many animal species such as bees, fish, birds, monkeys, salamander to mention some among many others [1, 35, 38, 40, 56, 81]. Therefore, these basic numerical abilities seem not dependent on enculturation or language as is demonstrated in a study with an indigene tribe of the Amazon has shown as well. This Brazilian tribe lives isolated in the jungle and has developed number words only for collections of one, two, three, four, and five items—everything beyond is simply labelled as many. Behavioural tests have shown that these people are able to perform approximate numerical tasks with concrete magnitudes comparable to us including magnitudes larger than five [73]. Finally, another very basic numeric capacity called subitizing is the simultaneous perception of small quantities up to five without counting [94]. However, recent findings have shown that the subitizing range in preschool children was only up to three and that the range can be larger by pattern recognition when dots are canonically presented [43, 55]. These numeric precursor abilities serve as foundation for the development of more sophisticated and enculturated numerical concepts (please see also Table 1).

Furthermore, numerical skills and representations are assumed to be acquired in a hierarchical and dynamic fashion [102]. Based on the representation of magnitudes, a verbal representation (number words) during preschool is followed by the establishment of a symbolic representation (Arabic digits) during schooling. Finally, spatial number representation is assumed to develop successively which is thought to resemble a number line in our mind and demonstrates that quantity is represented in a spatial nature [24]. In addition, behavioural evidence suggests that alike many other non-numerical (cognitive and non-cognitive) factors influence the maturation of numerical thinking such as working memory, language, spatial skills or attention which all are tightly linked to numerical development [for review, please see Kaufmann [49]]. A recent study has shown for instance that the level of executive functions and spatial skills in 3-year-old children predicts 70 % of the variance in later mathematics performance [100]. Moreover, Pina et al. [74] highlighted that different components of working memory (spatial and verbal) relate to different mathematical areas and that non-verbal intelligence and language may have different relationships depending on the mathematical area assessed.

The representation of the 'mental number line' is assumed to be influenced by cultural factors, like counting routine [34], the numerical system [85, 86], or reading direction [24, 106], as well as spatial routine, sensory and motor experiences [33, 66] and neuronal processes [34, 82]. Recent findings have even demonstrated that infants aged 7 months, who are far from gaining symbolic knowledge and mathematics education, show a preference for increasing magnitude displayed in a left-to-right spatial orientation [20]. Accordingly, most people in western cultures show a left to right oriented mental number line with a logarithmic scaling [23, 24]. However, with increased development and expertise in a certain number range, this scaling follows rather a linear function reflecting a more mature representation of numbers [58, 91].

During the early stages of the development of arithmetic competences, children solve arithmetic tasks by inefficient counting strategies also often reflected by the use of finger counting. Later on, after practicing and automatization, results can rather be retrieved from memory [92].

Taken together, present findings clearly show that numerical representations in children are modified and formed according to experience, increasing expertise and maturation of domain-specific and domain-general neuro-cognitive processes (please see also Table 1).

Definition of developmental dyscalculia

DD is a specific learning disability affecting the development of arithmetical skills with estimated prevalence rates between 3 and 6 % [52, 89] (see also Table 1). Recent studies claim that

Table 1 Summary of typical and atypical development of numerical skills, neuronal correlates of typical and atypical number processing, as well as relevant points in the definition and etiology, the diagnosis, and intervention of developmental dyscalculia

Development of number processing

		Typical	Atypical (Dyscalculia)
Behaviour	Precursor skills	▪ Innate number sense (discrimination between small quantities with larger distances)	▪ Impaired innate number sense
		▪ Increased quantity discrimination skills (larger quantities, smaller distances)	▪ Problems in quantity estimation
		▪ Subitizing	▪ Reduced subitizing range
	Number skills	▪ Mapping of different number representations (concrete quantity, number words, Arabic digits etc.)	▪ Inaccurate mapping and transfer of different number representations (more problems with symbolic representations)
		▪ Counting	▪ Counting difficulties, like backward counting
		▪ Place-value system	▪ No understanding of the place-value system
		▪ Mental number line representation (logarithmic -> linear function)	▪ Impaired development of or access to the mental number line
	Calculation skills	▪ Arithmetic by counting	▪ Stick to counting strategies by the usage of their fingers
		▪ Arithmetic by retrieval	▪ Often very limited retrieval
		▪ Arithmetic by decomposition (e.g. 6*8 = 5*8 = 40+8 = 48)	▪ Lack of understanding how to decompose difficult problems into easer ones
		▪ Acquisition of different calculation procedures and concepts	▪ No understanding of calculation procedures and concepts
Brain	▪ Complex fronto-parietal neuronal network: Parietal lobes (IPS), prefrontal cortices, regions associated with the dorsal and ventral visual pathways, sub-cortical areas and cerebellum. ▪ Maturation: Increased and more focal recruitment of brain areas associated with automated number processing, like the IPS or with numerical fact retrieval on left hemispheric perisylvian brain areas and the contribution of hippocampal-prefrontal circuits. Decreased reliance on supporting brain functions mainly located in the frontal lobes.		▪ Aberrant neuronal network: Differences in brain activation, grey and white matter volume, and fibre connections. Activation pattern less precise and main functional and structural deficits in core regions for number processing (parietal regions). Other cortical and subcortical regions that contribute to numerical cognition can be affected. Stronger recruitment of supporting areas associated with working memory, attention, monitoring, updating or finger representation might reflect compensatory mechanisms.

Developmental dyscalculia

Definition & Etiology	▪ Heterogeneous learning impairment affecting numerical and/or arithmetic functioning at behavioural, psychological and neuronal levels ▪ Persistent into adulthood ▪ Hereditary and environmental components are hypothesised as possible causes ▪ Prevalence: 3–6 % ▪ Gender distribution: females > males, but findings are still inconsistent ▪ Comorbidities: very common, like attentional problems (ADHD), dyslexia, anxiety, visuospatial impairments, spatial working memory problems etc.
Diagnosis	▪ Early identification, diagnosis, and treatment is very important ▪ Detailed description of strengths and weaknesses by multi-dimensional assessments tracking: ◦ Numerical and arithmetical processes ◦ Domain-general abilities ◦ Neurological, sensory, and motor processes ◦ Socio-emotional and social functioning ◦ Medical, educational, and family history ▪ Difficulties must persist over longer time periods
Intervention	▪ Adapted to individual profile of performance levels and difficulties ▪ One-to-one training ▪ Structured and hierarchically built ▪ Basic non-curricular and curricular numerical topics. ▪ Many repetitions ▪ Motivation is stimulated by reward and reduction of math anxieties

more girls than boys are affected [32], but literature is still controversial, and also, opposite findings have been reported [27, 76]. Independent of gender, DD seems to be an enduring learning disorder persisting into adulthood [54, 88] with hereditary as well as environmental components being discussed (see also Fig. 1) [2, 8, 87]. A recent first large-scale genetically sensitive investigation of number sense has even revealed that basic numerical understanding is only modestly heritable (32 %), with individual differences being rather explained by environmental influences (68 %) [97].

DD is a heterogeneous disorder resulting from individual deficits in numerical or arithmetic functioning at behavioural, cognitive/neuropsychological and neuronal levels [50, 80]. However, it has to be considered that arithmetic difficulties can reflect individual differences in both numerical and non-numerical functions (see Fig. 1). Children with DD have problems in the mastery of a wide range of numerical understanding such as counting skills, magnitude processing, arithmetic, transcoding between number words, digits and quantities, the spatial number representation, or more domain general skills like working memory or attentional processes (see also Fig. 1). In particular, visuo-spatial working memory seems to be impaired in children with DD [5, 78, 96] (Vignette 1).

Generally, multiple problems are most common and pure DD apply to a minority of cases only. Rubinsten and Henik [80] propose different frameworks for the origin of DD or mild learning disabilities and their cognitive deficits. First, a unique core deficit in processing numerosities is assumed because of a unique pathophyhsiology. Butterworth et al. [14] similarly emphasize a core deficit in understanding sets and their numerosities, which the authors claim to be fundamental to all aspects of elementary school mathematics. However, present research challenges a unique cognitive deficit as possible cause of DD. For instance, Rouselle and Noel [79] found that children with mathematical disabilities were only impaired when comparing Arabic digits, but not when comparing non-symbolic magnitudes. Also, in typical development, children's efficiency to process symbols seems to be important for the development of their arithmetic fluency above and beyond the influence of non-symbolic number processing skills [9]. Finally, a single restricted biological deficit as origin of DD is not in line with current neurobiological findings which indicate functional and structural abnormalities in a widespread network across cortical and subcortical brain regions [31, 60]. Therefore, other frameworks taking the heterogeneous behavioural deficits, the common occurrence of co-morbidities and neuronal underpinnings of

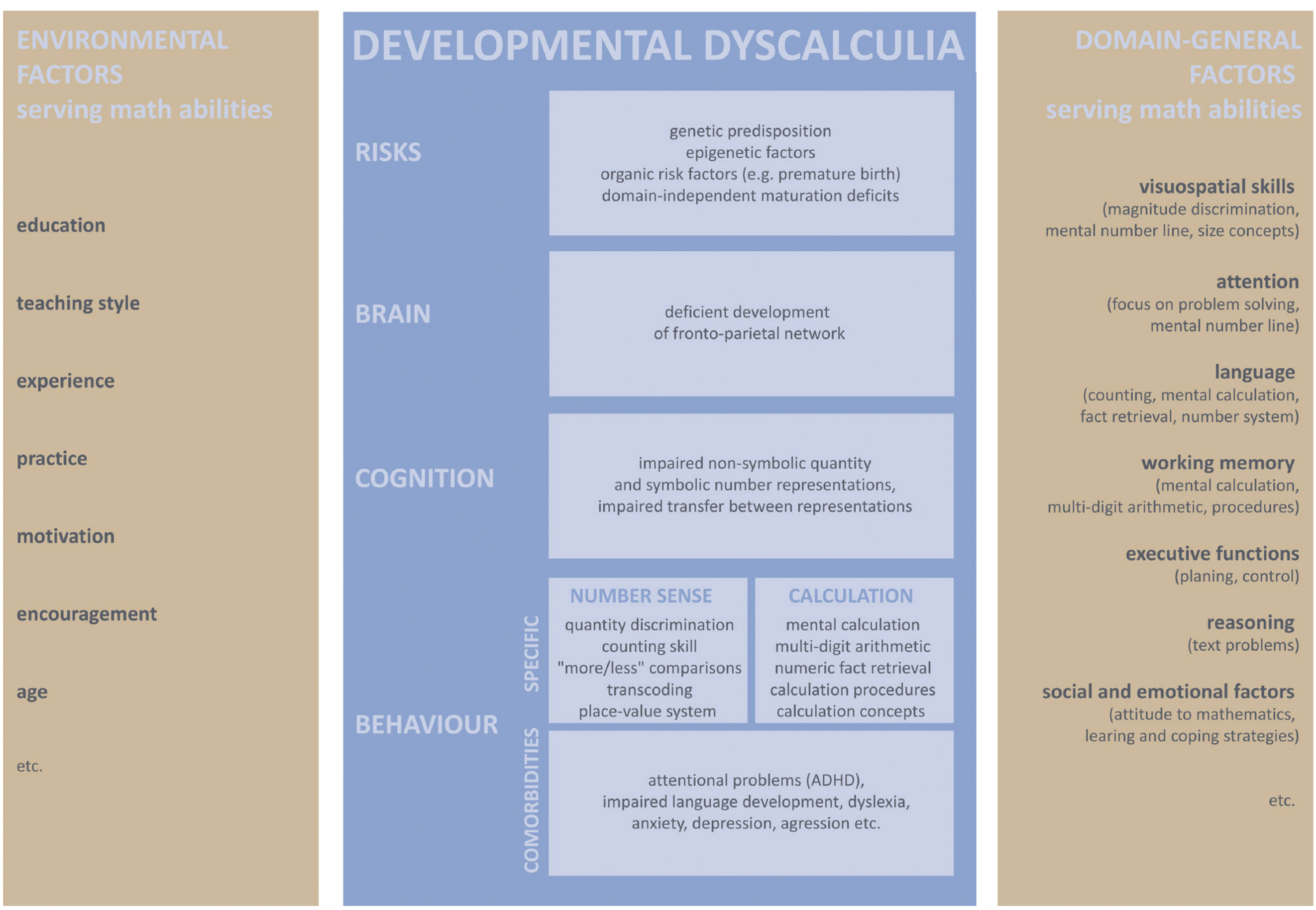
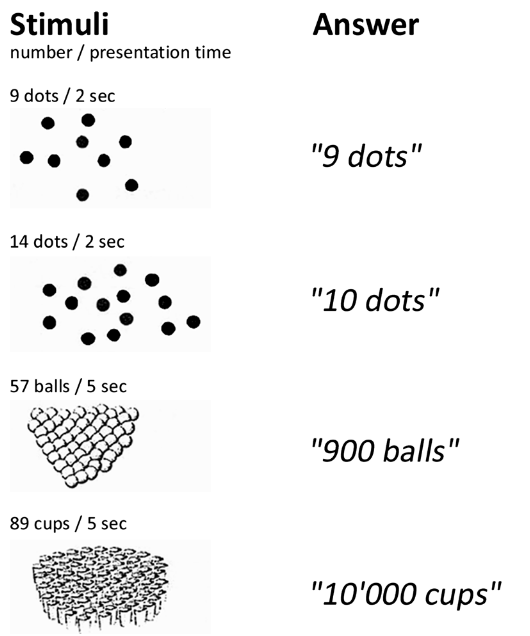
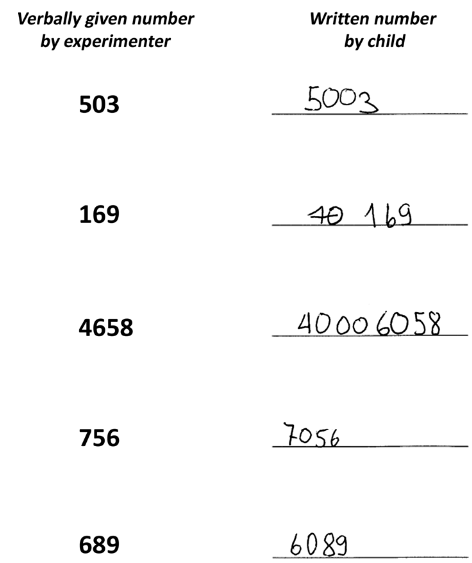


Fig. 1 Potential factors and different levels on which developmental dyscalculia can manifest itself (Fig. 1 is adapted from [52])



Vignette 1 Impaired magnitude representation—dyscalculic boy, 11 years, 5th grade. This boy showed severe problems in the estimation of concrete quantities. The task was to estimate the number of dots, balls or cups, respectively, which have been shown only for 2 or 5 s. He was able to estimate small quantities like nine dots, but failed with larger quantities. For instance, he estimated 57 balls as 900, or 89 cups as 10,000. This clearly shows that this boy has no understanding of large quantities and big numbers. They are just a lot, and 900 or 10,000 are a big number. Illustrated is a copy of the original protocol of the subtest number 9 'quantity estimation' of the ZAREKI-R [103]



Vignette 2 Impaired transcoding and place value system—dyscalculic girl, 8 years, 3rd grade. Numbers were dictated verbally and the girl had to write down the corresponding Arabic digit. For illustration, the verbally given numbers are listed on the left side to the notes of the girl. She shows difficulties in the verbal to Arabic transcoding and the understanding of the numerical place value system. Illustrated is a copy of the original work sheet of the subtest number 3 'transcoding' of the test battery ZAREKI-R [103]

DD into account are rather plausible. As alternative origin, Rubinsten and Henik (2009) suggest that multiple cognitive deficits in DD might be explained by multiple brain dysfunctions or that dysfunction in a central brain area could result in multiple cognitive or behavioural manifestations (Vignette 2).

As described, arithmetical difficulties are often associated with other learning problems (dyslexia, ADHD). Probably as a consequence of these multiple learning difficulties found in DD, many children develop additional psychiatric disorders, like anxieties, depression or aggressive behaviour. It has to be taken into account that especially such secondary symptoms of DD can lead to general refusal and impairments in other school topics (see Kohn, Richtmann et al. 2013 for a new math anxiety questionnaire for German speaking children). Finally, also on a longer timescale, it has been shown that low math abilities have serious negative impact on professional careers [72].

In sum, number processing comprises a multitude of different numerical and non-numerical competencies, and children with DD differ in their individual profiles of strength and weaknesses in these skills. Therefore, also, the diagnosis of DD should be based on multi-dimensional assessments tracking different numerical and arithmetical processes and relevant domain-general abilities as well as neurological and socio-emotional functioning.

Diagnosis of developmental dyscalculia

According to Kaufmann and von Aster [52], a detailed diagnostic evaluation is needed when dyscalculia is suspected in order to take proper account of the complexity of this learning disorder and to produce an accurate picture of the affected child's particular strengths and weaknesses in the area of numbers and calculations (see also Table 1). In view of the multiplicity of the functional components participating in this learning disorder and the wide range of potential mental and neuropaediatric comorbidities, it is clear that the diagnostic evaluation must go beyond the strictly mathematical components to include a thorough personal, familial and scholastic developmental history. The evaluation of the child's general cognitive development must consider non-numerical cognitive domains, social factors, emotional well-being and, where appropriate, findings from neurophysiology (neurology and neuroimaging). Furthermore, not only at school age, where most of the children who struggle with numbers and calculation are diagnosed, but at a much earlier time point, potential children at risk could be identified. In children of kindergarten age, specific precursor skills can be identified that have been found to be reliable predictors of later calculation abilities [7, 95]. For instance, the understanding of quantity, subitizing, mastery of counting skills or the identification of Arabic numerals can already be impaired in preschool children. However, not every child that is conspicuous in any of these number competencies at preschool age must develop DD. At this early age, it has to be taken into account that the scope of development is wide, and therefore, children differ also in the mastery of numerical skills. Hence, some children might simply be slow learners but not necessarily dyscalculic (Vignette 3).

Current revisions of international classification manuals take the heterogeneous character of DD into account which is reflected in changes in conceptualizing learning disorders in general. In the International Classification of Diseases (ICD 10th revision) of the World Health Organization [71] as well as the former version of the Diagnostic and Statistical Manual of Mental Disorders (DSM 4th revision) of the American Psychiatric Association [3], DD has been defined as a domain-specific learning disorder that emerges at an early stage of development and cannot be explained by inappropriate schooling or deficient learning opportunities. Domain specificity commonly has been described by a discrepancy between general intelligence and specific ability. This concept implies a rather static and endogenous origin of the disorder, which is challenged by recent research and theory that addresses the

Vignette 3 Impaired number meaning—girl, 8 years, 2nd grade. 'At second grade, teachers told Irma's parents that their 8-year-old child had severe dyscalculia, verified by a test of mathematical achievement. Reading and spelling skills had been excellent. Irma developed a deep aversion to mathematics and was absolutely convinced that she would never learn arithmetic. She also showed increasing symptoms of depression and reluctance to attend school. She was, however, able to compare the magnitude of different amounts of objects, indicating that core-system abilities were intact. Irma had above average verbal and nonverbal intelligence and she engaged in rich and imaginative play. At about 3 to 4 years of age Irma started to invent a fantasy play, a kind of fairy tale in which the protagonists, unfortunately, had numbers for names. During therapy sessions she would paint and give detailed biographies of all the persons in her fantasy world: 'Three' was a lovely boy, but sometimes cheeky to his mother. He had two friends in his neighbourhood, 'nine' and 'twenty-three', with whom he did a lot of silly tricks, and so on…' [102]. A closer look at her drawings also revealed that they were full of numbers. No wonder she got into trouble when she was asked by the teacher to subtract 3 from 9. Irma's case demonstrates her extensive use of numbers for non-numerical assignments and associations were only detected by careful exploration of her learning history and that a conventional dyscalculia screener might would have classified her as dyscalculic by mistake

nature of general intelligence (IQ) and the power of environmental factors, ranging from cultural circumstances (e.g. nature and extent of schooling, nature of the counting system) to the effects of pre-/post-natal illness or socio-emotional adversity [50, 60]. In addition, there is growing empirical evidence that children with numerical difficulties and average as well as below average intellectual levels show identical patterns of difficulties in math learning [29, 67]. It has also to be kept in mind that numerical understanding, mathematical capabilities and general cognitive skills measured by intelligence tests are partly overlapping constructs [for more detailed discussion please see Ehlert [29]]. Many intelligence test batteries include sub-tests requiring numerical abilities. Therefore, it is very difficult, if not impossible, to disentangle cognitive functions related to number processing and/or testmetric intelligence. In addition, the constructs of testmetric intelligence used in IQ tests differ widely according to the extend they require number knowledge, arithmetic or mathematical reasoning. Finally, children with low general intelligence scores could hardly meet a discrepancy criterion because they would need to have extremely low math performance scores. Accordingly, in the recently published 5th revision of the DSM [3], the specific developmental disorders of scholastic skills have been grouped together as dimensions within a single category, in each of which there can be a greater or lesser degree of impairment; the psychometric demonstration of a discrepancy to otherwise normal intelligence is no longer required. This change has been introduced to take better account of the heterogeneity of these disorders with respect to performance profiles and comorbidities, and thus to improve the clinical utility of the diagnoses.

A recent approach focused on diagnosing DD on the basis of reliable single case brain imaging methods [28]. Despite the promising results obtained in this study, the authors emphasized that brain-based diagnostics are not as good as standard diagnostic tests that are based on behavioural measures only, but as the following sections demonstrate, might be a valuable extension in near future.

Neuronal correlates

Subsequent sections should provide insights into the neuronal correlates of typical adult number representations and of arithmetical processing as well as the important differences to developmental neuronal systems in children. In the last section, neuronal underpinnings of DD will be pinpointed which demonstrates that DD is related to atypical development of numerical representations in the brain.

Numbers in the brain

During the last few years, a clearer picture has emerged of functional processes in the typical adult brain during number processing and calculation by means of contemporary brain-imaging techniques. These findings revealed an entire neuronal network necessary for number processing. Dehaene et al. [22, 26] proposed in his 'triple-code model' the distinction between an analogue magnitude representation mediating semantic number processing (i.e. numerosity) in the parietal lobe, a verbal-phonological number representation supporting verbal counting and number fact retrieval in left perisylvian areas and a visual-Arabic number representation represented by strings of digits including areas associated with the ventral visual stream.

Within this distributed network, the intraparietal sulcus (IPS) has been confirmed as the core locus of numerical processing. The IPS is activated whenever numerical magnitude is implicated, even in the absence of numerical task demands [for review please see references 15, 48, 70]. Furthermore, recent findings of single-cell recordings in monkeys revealed neurons in the IPS, which fire predominantly for a certain numerosity. Moreover, groups of neurons encode either the number in one or another modality (e.g. auditory pulses vs visual items), or both. Neurons responding to numerosity irrespective of the sensory modality support the notion of a supramodal neuronal code of numerical quantity [69].

As a nature of numerical cognition, the neuronal network engages also brain regions associated rather with domain-general capacities like memory, attentional, perceptual, motor and spatial functions. Particularly, the prefrontal cortex has been associated with general cognitive processes with emphasis on its role in monitoring, strategy choice, planning or manipulating information, as required in calculation tasks [18].

Taken together, number processing and calculation are a demanding cognitive ability which is processed by a complex neuronal network. In addition to the key areas for numerical cognition located in the parietal lobes, prefrontal cortices, regions associated with the dorsal and ventral visual pathways, as well as sub-cortical areas and the cerebellum play a significant role in numerical tasks [for review see reference 4]. In Fig. 2, top view of the typical fronto-parietal activation pattern found in adults is illustrated on the right side.

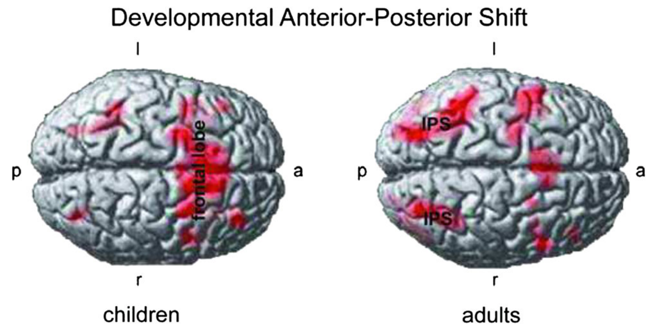


Fig. 2 *Top view* of typical fronto-parietal activation network for number processing in children (*left*) and adults (*right*). An ontogenetic shift from mainly frontal to task specific regions in the intraparietal sulcus (*IPS*) can often be observed. *a* anterior, *p* posterior, *l* left, *r* right. Illustration is based on data of Kucian, von Aster, Loenneker, Dietrich, and Martin [63]

Typical development of number representations in the brain

During development, neurocognitive systems are still immature, and functional differentiation of specific brain regions has not yet taken place or is not yet completed in children [10, 44, 49, 59]. With respect to the development of numerical cognition, it has been argued that with increasing age and experience, number representations and their interconnections undergo qualitative changes [59]. It seems plausible that a core region for number processing might consist of highly interconnected neurons for different numerical inputs. If so, activation of one neuronal population could quickly spread to other populations, leading to cross-notational activation. With development and higher numerical proficiency, these cross-notational activations probably increase, reflecting automatization of numerical processes. Therefore, a direct comparison of mature and developing brain systems may not be feasible due to considerable differences regarding brain structure and function.

Converging evidence suggests an anterior-posterior shift of brain activity associated with number processing and arithmetic during development (please see also Table 1). These changes are thought to reflect decreasing reliance on domain-general supporting (frontal) processing mechanisms and increasing functional specialization of number-relevant (fronto-parietal) brain regions [49]. Moreover, the effectiveness of calculation potentially depends on the development of more sophisticated strategies requiring automated retrieval of arithmetical facts and processing of quantities as well as Arabic digits. These maturational changes are reflected in differences in performance and accompanied brain functions. On the one hand, an increased and more focal recruitment of brain areas associated with automated number processing, like the IPS, is suggested due to more automatic processing of numbers. And, on the other hand, the stronger reliance on numerical fact retrieval is assumed to be reflected by an increased activation of left hemispheric perisylvian brain areas and the contribution of hippocampal-prefrontal circuits [16, 17].

The brain of dyscalculics

Convergent evidence is growing that DD has a particular neuronal correlate [for review see book chapter, e.g. by Kucian 60]. Despite the relatively high prevalence of DD, only very little imaging studies have addressed the question of neuronal attributes of this learning deficit. Nevertheless, existing findings could demonstrate that in children suffering from DD, the typical developmental trajectories seem to be deficient and might be explained by neuronal deficits (please see also Table 1).

On the one hand, neuronal underpinnings of DD are designated by aberrant brain activation [75, for review see book chapter, e.g. references 6, 60, 61] and macro- [77, 83] as well as micro-structural [57, 83] deficits in core areas for number processing mainly located in parietal areas [for review see reference 53]. On the other hand, also compensatory mechanisms can be observed in children with DD which are reflected by increased reliance on supporting brain functions related to domain general cognitive abilities [51, 62].

Aberrant brain functions

Regarding brain activation, there is consistent evidence that DD is associated with abnormal parietal activity patterns indicating a deficient neuronal representation of numerosity. A couple of studies showed a general *reduced brain activation* in these core areas for number processing [11, 58, 61, 78]. Additionally, there is growing evidence that impaired numeracy might also be due to deficits in other brain regions. In particular, several imaging studies reported reduced brain activation in distributed areas of the frontal lobe, occipital areas and deep brain structures [53, 58, 61, 62, 68, 75, 78]. Although reported findings base on different numerical tasks which range from rather basic number sense [non-symbolic distance effect 75], to the understanding of ordinality [58], to symbolic number comparison [68], to arithmetic [multiplication or approximate addition, 11, 61], or to non-numerical skills that are processed by overlapping networks [spatial working memory, 78], coincident reduction of brain activation in the fronto-parietal network has been reported.

In contrast to reduced brain activation, children with DD also tend to show *increased brain activation* in mainly frontal areas, but also parietal regions, probably as a consequence of compensatory processes due to their deficits [51, 62, 68]. Again, the development of possibly compensatory mechanisms seems to be independent of tasks, since both non-symbolic [51, 62] as well as symbolic number processing [68] evoked such increases in brain activation in children with DD.

Numerical tasks with varying difficulty levels induce usually an increased brain activation for more complex problems [e.g. 75]. However, brain activation in people with DD seems not do be modulated in the same way as found in typically developing subjects. Some studies demonstrated a *lack of modulation* of parietal brain activation related to task complexity with greater activation for more difficult problems in DD [6, 21, 68, 75, 93]. Furthermore, similar to the lack of brain modulation in parietal areas, Berteletti et al. [11] described an absence of brain modulation by problem size in verbal regions, suggesting that children with math difficulties do not consistently retrieve solutions verbally even for smaller problems. In terms of reported difficulties in spatial working memory in DD, Ashkenazi et al. [5] showed that children with math difficulties show no modulation brain activity during arithmetic problem solving related to visuo-spatial working memory performance. The authors conclude that, unlike typically developing peers, children with math difficulties do not use visuo-spatial working memory resources appropriately during arithmetic problem solving.

Differences in grey and white matter volume

Besides of abnormal brain functions, also morphometric differences between typically developing children and children with DD have been reported [57, 77, 83]. Regarding macro-structural differences, DD is characterized by reduced grey and white matter volume in areas (parietal areas, in particular the IPS) that are supposed to play a key role for domain-specific development of numerosity. In addition, reduced grey and white matter volume was found in regions (frontal and subcortical areas) important for the development of domain general abilities [77, 83].

Atypical neuronal fibre connections

Successful cognitive performance relies on the development and formation of well-organized networks in the brain. Fast and adequate connections between different brain regions are crucial for efficient transfer and adjustment of information. Micro-structural deficits are related to aberrant fibre connections between brain regions. To date, only very little knowledge is available regarding specific impairments of brain connections as possible neuronal correlates of DD [57, 83]. However, existing findings highlighted a connection deficit between parietal and frontal areas in children with DD. In particular, the superior longitudinal fasciculus (SLF) seems to be affected in parts that are adjacent to the IPS [57]. Reasons for micro-structural alterations in the SLF are speculative but might reflect deficient myelination of fibres rather than axonal development [for review please see references 64, 104]. Nevertheless, results clearly demonstrate that not only the IPS but also the intact connection of parietal areas with the frontal and temporal cortex through the SLF seems to be essential for number representation [57, 98, 99].

In sum, regarding this wide range of reported abnormalities in neural networks for number processing and calculation in DD, it is difficult to draw a clear picture, but upon existing literature, it can be concluded that the activation pattern of children with DD is less precise and main functional and structural deficits are apparent in core regions for number processing, which mainly comprise parietal regions. However, also other cortical and subcortical regions that contribute to numerical cognition can be affected. The stronger recruitment of supporting areas associated with working memory, attention, monitoring, updating or finger representation are supposed to reflect compensatory mechanisms in dyscalculic children, but could also reflect deficits in these domain-general skills which might contribute to the development of DD. As a consequence, observed heterogeneity and comorbidity in DD are a natural outcome of such a multicomponent neuronal system responsible for efficient number processing [31].

Intervention

Ambitious efforts are needed to transform basic knowledge about neurocognitive development of number processing into evidence-based practical applications for special needs education and therapy. So far, only few attempts have been conducted to incorporate current neuropsychological knowledge into the development of interventions for children with math difficulties [for review see reference 19]. However, as concluded by these authors, interdisciplinary approaches that include psychology, neuroscience, and education could contribute to optimal designs for interventions targeting neurocognitive mechanisms and can furthermore evaluate the efficacy of such interventions at the behavioural and brain level. In general, specific intervention of children or adolescents with math difficulties can help if the intervention is designed in an effective way. Ise and Schulte-Körne [42] conducted a meta-analysis to distinguish which factors make an intervention effective. The authors distinguish between curricular trainings, focussing on school material and non-curricular interventions, which mainly train basic numerical understanding. Results provide evidence that an intervention is most successful (see also Table 1):

- In a single training (not group wise or in class)
- When it is adapted to individual performance levels
- When it is structured and hierarchically built
- When it includes basic non-curricular as well as curricular numerical topics
- When it consists of many repetitions
- When motivation is stimulated by reward and reduction of math anxieties.

Regarding the two latter factors, computer-based interventions may provide valuable contributions as they have the advantage that children generally like to work with the computer and that this setting is free from any social pressures fostering math anxieties.

Based on our previous research, we have developed and evaluated a computer-based training program for children with DD with the aim of improving number representations and strengthening the link between numbers and spatial processes on the internal mental number line [58]. Results have indicated that children with and without DD improved their arithmetical abilities and spatial number representations. Additionally, the training resulted in a modulation of brain functions (see Fig. 3): After completion of the training, a reduction in the recruitment of brain regions relevant for numeracy, including mainly frontal areas, left IPS and the left fusiform gyrus was observed in both control children and children with DD. A decrease of brain activation in these regions and particularly of the frontal lobe is assumed to reflect automatization of cognitive processes necessary for mathematical reasoning [105]. Furthermore, a significant increase of activity in bilateral parietal areas, including the IPS, was found in children with DD 5 weeks after completion of the training. In conclusion, domain-specific game-like interventions are associated with neuroplasticity in functional circuitry that is impaired in children with DD, and moreover, they can positively influence brain activation that is atypical into more typical brain activation.

Based on these positive results, we have further developed and extended the training. The new version is called *Calcularis* and combines the training of basic numerical cognition with the training of arithmetical abilities in a wider number range [45–47, 101]. *Calcularis* includes multiple games in a hierarchical structure which aim to train different numerical and arithmetical aspects based on current neurocognitive models of numerical cognition [22, 25, 59, 65, 102]. Competencies such as subitizing, non-symbolic numerical magnitude judgements, understanding the number system, transcoding between number words, magnitudes and Arabic digits, number line comprehension, expressions like bigger/smaller, more/less or add/subtract, ordinality

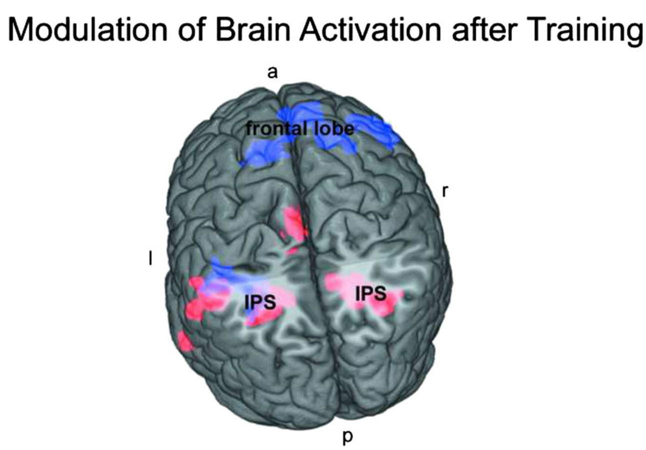


Fig. 3 Modulation of brain activation after computer-based intervention in children. *Blue* decrease of brain activation in predominantly supporting functions in the frontal lobules in children with and without DD. *Red* increase of brain activation in task-related regions in the parietal lobules in children with DD after a 5-week rest period. Illustration is based on data of Kucian, Grond et al. [58]

principles, addition, subtraction, multiplication, or division are trained. Based on so-called dynamic Bayes-nets, *Calcularis* is highly able to adapt to the particular needs of each individual child and in that way offers supporting learning conditions on the grounds of individual profiles of numerical problem solving skills. This is also reflected in the outcome after 6 or 12 weeks of training: Children improved their arithmetical, especially subtraction skills supporting the notion of better mathematical understanding and a shift to increased and more sophisticated fact retrieval strategies. In addition, Käser et al. [45] reported that children performed better in a number line task after the training. In the number range between 0 and 10, the deviation from the correct position was reduced by 33 % after 6 weeks. Children especially also reduced the variance of the distance between the correct and the indicated location of the number on the number line (medium-large effect size). The authors argue that better performance in the number line task indicates refinement of the internal mental number line and more accurate access to it and confirms the results of previous studies [12, 39, 90] which demonstrated significant correlations between arithmetical learning and the quality of numerical magnitude representation.

Taken together, intervention programs which are carefully developed adaptive to individual learning profiles and based on current knowledge of neuropsychology and brain imaging findings of numerical cognition provide a helpful tool for children with math difficulties or DD. They have the power to improve the understanding of numerical concepts and modulation of corresponding brain functions. However, these computer interventions should be seen as supplementation to conventional learning therapies since individual therapy by trained dyscalculia therapists seems still more effective [41], and the focus should mostly lie on optimal teaching and learning environment for children in general.

Open questions and future directions

As outlined in the present review, our knowledge and understanding of behavioural and neuronal characteristics, as well as, the general awareness of DD in our society, have constantly increased over the last decade. Although we are gaining a clearer picture of this learning disability, still many questions are unsolved, reported findings are sometimes contradictory and generate new questions.

Generally, we think that we have arrived at a stage, where we should expand our view angles on dyscalculia:

First, the artificial restriction of most research on pure DD is missing the point that DD children with additional comorbidities are rather the rule and not the exception. Although it is essential to keep your examination cohorts as homogenous as possible to draw clear conclusions, future research should more focus on children who reflect rather reality, namely DD children with comorbid disorders. In the same context, it might push the level of understanding DD to a next step by not pooling all children with DD together. Instead of, according to the heterogeneous character of DD, a division into different sub-groups with more homogenous difficulty profiles would probably pinpoint underlying causes and behavioural consequences more precisely.

Second, current findings from neuroscience clearly illustrate that number processing and calculation is processed by the integration of different co-activated networks in our brain. On the one hand, empirically grounded knowledge highlighted the important role of the IPS. On the other hand, there is a wide range of reported, but up to now mostly neglected, differences in brain function or structure in many other cortical and subcortical brain areas between typical and atypical developmental trajectories. Therefore, future studies should bear also other brain regions apart from the parietal lobe in their focus.

Third, when we are thinking of atypical developmental trajectories present in DD, longitudinal studies would provide the potential of delineating the course of DD in a more realistic way than currently conducted cross-sectional studies. Ideally, such studies would tap the state of behavioural and neuronal progress at several time points to follow the developmental function, which might not be linearly, as accurate as possible.

Fourth, it is still unclear to what extent the link between included brain regions in number processing and calculation might explain the neuronal deficits in DD. In other words, future studies should go beyond the mere localization of abnormalities and offer information on connectivity between brain networks and how such networks differ between groups of individuals.

Fifth, present methods allow us to gain insights into DD from different perspectives, such as brain function, brain structure, brain metabolism or time course of neuronal processes by means of electrophysiology. The challenge now will be to integrate these findings by multi-dimensional approaches in DD. Such examinations will be very demanding but provide the chance to define clearer models of underlying problems.

Sixth, effects of secondary symptoms like specific math anxiety have been disregarded to a vast degree in behavioural studies, the investigation of neuronal underpinnings and also in intervention studies. However, on the grounds that many children with DD suffer from accompanied anxieties, one should not neglect the significant negative effects of anxiety symptoms on learning. Moreover, it is unclear to what extent observed brain activation increases or decreases, or even brain structural alterations are due to elevated anxiety levels or corresponding emotional control mechanisms.

Finally, our future efforts should pursue the goal to improve the appropriate support of children with DD. This would start with a uniform definition and diagnosis of DD, followed by a regulated compensation of any disadvantages and individual therapy which takes the heterogeneous profile of each child into account.

Conclusion

DD is a complex and heterogeneous phenomenon that affects different components of mental development and requires interdisciplinary research, remediation and therapy. The neurocognitive development of number representations and calculation abilities is interconnected with the development of other cognitive domains and domain general abilities like attentional and behavioural control and working memory, but is also associated and intertwined with individual experiences in individual environments. Therefore, assessments of different numerical and non-numerical skills should be completed including a careful exploration of the individual learning history.

Conflict of interest We, Karin Kucian and Michael von Aster, certify that there is no conflict of interest with any financial organization regarding the material discussed in the manuscript.

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