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Review article

Evaluation of the Triple Code Model of numerical processing—Reviewing past neuroimaging and clinical findings

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ABSTRACT

This review reconciles past findings on numerical processing with key assumptions of the most predominant model of arithmetic in the literature, the Triple Code Model (TCM). This is implemented by reporting diverse findings in the literature ranging from behavioral studies on basic arithmetic operations over neuroimaging studies on numerical processing to developmental studies concerned with arithmetic acquisition, with a special focus on developmental dyscalculia (DD). We evaluate whether these studies corroborate the model and discuss possible reasons for contradictory findings. A separate section is dedicated to the transfer of TCM to arithmetic development and to alternative accounts focusing on developmental questions of numerical processing. We conclude with recommendations for future directions of arithmetic research, raising questions that require answers in models of healthy as well as abnormal mathematical development.

What this paper adds: This review assesses the leading model in the field of arithmetic processing (Triple Code Model) by presenting knowledge from interdisciplinary research. It assesses the observed contradictory findings and integrates the resulting opposing viewpoints. The focus is on the development of arithmetic expertise as well as abnormal mathematical development. The original aspect of this article is that it points to a gap in research on these topics and provides possible solutions for future models.

1. Introduction

Over the past decades of research on arithmetic, TCM has become predominant in sketching the processes underlying arithmetic expertise and their interactions; however, the model is based on findings from educated adults and hence lacks specific explanations applicable to the development of arithmetic and to mathematical problems in DD (Kaufmann et al., 2013). In addition, few neuroimaging studies systematically tested TCM (according to Prado, Mutreja, & Booth, 2014), and the interaction of brain maturation and arithmetic education in healthy and dyscalculic children has not been clarified sufficiently (see Kaufmann, Wood, Rubinsten, & Henik, 2011 for a developmental calculation model based on a meta-analysis). The primary purpose of this review is to contrast those findings supporting the model with conflicting results from behavioral, clinical, neuroimaging, connectivity, and developmental studies conducted over the last 20 years. Moreover, a separate section is dedicated to developmental considerations and abnormalities evident in DD. The review aims at evaluating the current state of knowledge regarding TCM and provides possible reasons for contradictory findings. It finishes by outlining open questions as well as future perspectives focusing on applications that appear to be relevant in the diagnostics as well as interventions of DD.

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2. Scope of the present review

This review is an attempt to evaluate TCM from various perspectives in the fields of numerical processing and of basic arithmetic. We sought to compile findings from what we believe are the predominant questions in the literature, namely

(a) How are basic arithmetic operations solved?
(b) What are the roles of magnitude processing and arithmetic fact retrieval?
(c) What are the neural bases of the single arithmetic operations?
(d) How are brain regions involved in numerical processing connected?
(e) How do numerical processing and arithmetic develop?
(f) How can TCM be applied to healthy and abnormal arithmetic development?

These questions are addressed in the sections 'Empirical Evidence on TCM' (a to d) and 'Dyscalculia and TCM' (e and f). In addition, we elaborate on 'Possible reasons for discrepant results ", finishing with suggestions for 'Features of a comprehensive model of arithmetic development".

While we do believe that we have gathered the most relevant streams of research, providing opposing viewpoints for each, the present review is not systematic. We do not claim to provide an exhaustive overview of studies on arithmetic processing and TCM. Still, our review may initiate new ideas of thinking about numerical processing and lead to further elaborations on TCM when it comes to developmental aspects and abnormal development of arithmetic.

3. The Triple Code Model of number processing

3.1. Key aspects of TCM

Numerical processing is a complex skill involving several interrelated mechanisms such as understanding arithmetic principles or memorizing and retrieving arithmetic facts (Kaufmann et al., 2013). A clear-cut distinction has emerged between a system of calculation procedures based on quantity on the one hand and a second calculation system resting on memorized facts (Dehaene & Cohen, 1991). Incorporating this idea, TCM (Dehaene, 1992; extensions: e.g. Dehaene & Cohen, 1995; Dehaene & Cohen,1997) is a multiroute model of numerical processing postulating three functionally independent but interrelated codes (Dehaene, 1992). According to TCM, the semantic content of numbers (i.e. the meaning) is represented by an abstract magnitude module (M1, Dehaene & Cohen, 1995), whereas asemantic information is processed in two distinct modules, one for verbal numerical information and the other for written number words and Arabic digits (M2 and M3 respectively, Dehaene & Cohen, 1995). Together, M1 and M2/M3 represent separate but connected calculation systems (e.Dehaene, 2007).

Central to TCM is an assumed functional independence between notation types (Arabic digits vs. number words, see Knops, 2016) as well as the necessary transcoding pathways between the three codes (Dehaene & Cohen, 1995; Dehaene & Cohen, 1997). Thus, there is a direct route for converting visually presented input to verbal output and vice versa (M2; M3) independent of the semantic meaning (M1) of its quantity. Moreover, an indirect route processes the mental representation of quantity (Dehaene & Cohen, 1997). Depending on modality (visual vs. auditory see Knops, 2016) and notation, numerical content activates either M2 (i.e. verbal number words) or M3 (i.e. Arabic digits) or both, and may converge on the automatic activation of M1 which registers the associated numerical cardinality (Dehaene & Cohen, 1995; but see Wong & Szucs, 2013 contradicting automatic activation of quantity processing).

TCM predicts distinct paths of number processing depending on task complexity and the respective input, the mental operations carried out, and the resulting output. Consolidated arithmetic operations putatively become stored in long term memory and enable fast responses to simple arithmetic problems – potentially from an internal multiplication table (Krueger, Landgraf, van der Meer, Deshpande, & Hu, 2011). Thus, an efficient strategy to solve familiar multiplication problems especially of larger quantities is apparently to retrieve solutions from memory rather than by using calculation procedures (e.g. Zamarian, Ischebeck, & Delazer, 2009). As arithmetic facts are accessed linguistically, this process involves verbal phonological processing (M2) independent of the mental representation of magnitude (M1, see Moeller, Klein, Fischer, Nuerk, & Willmes, 2011).

Depending on task requirements, arithmetic problem solving can be exact or approximate (Klein, Nuerk, Wood, Knops, & Willmes, 2009), leading to distinct TCM pathways. In keeping with Dehaene and Cohen (1997), exact solutions to novel problems mandatorily involve calculation procedures and therefore activate verbal numbers (M2) or digits (M3). Exact calculation and fact retrieval are interrelated in that rehearsed arithmetic procedures (exact calculation) lead to strong associations between problem and solution in long term memory, allowing subsequent retrieval (Klein et al., 2016). As well, both share a common dependence on language (Rapin, 2016). By contrast, approximating a number range may be achieved by evaluating its cardinality using the so-called innate number sense (Dehaene & Cohen, 1997) or approximate number system (Cantlon, Platt, & Brannon, 2009), represented by M1 in TCM. Dehaene and Cohen (1995) assume that more complex arithmetic operations require "semantic elaboration" of the problem's magnitude, i.e. access to the cardinal meaning of the numbers. This may enable the recoding of the problem into simpler operations that are each solvable through fact retrievable. Therefore, fact retrieval and magnitude processing often go hand in hand in TCM.

To sum up, TCM is a multiroute model with distinct semantic and asemantic representations of numerical content accounting for double dissociations between arithmetic operations depending on input and output format.

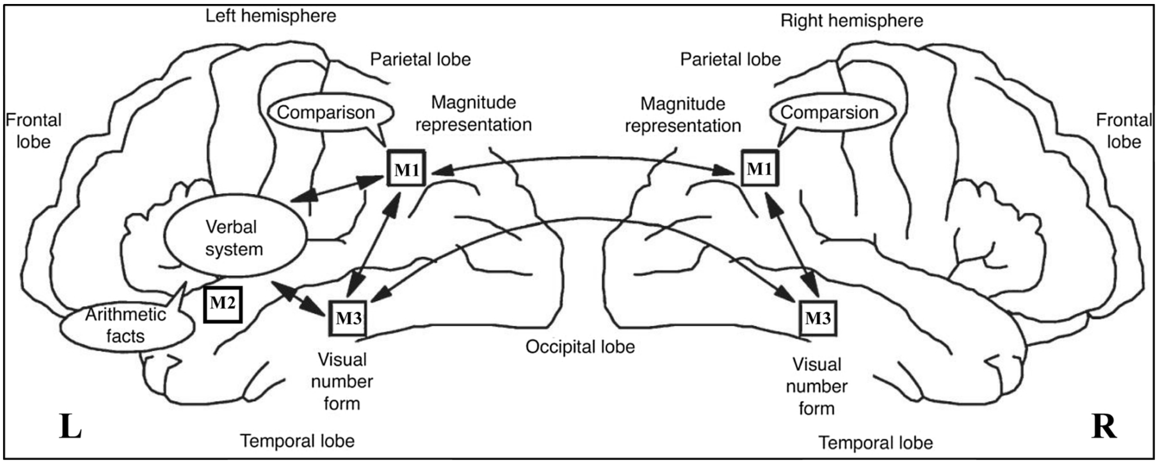

Fig. 1. Schematic Integration of Functional and Anatomical Assumptions of the Triple-code Model (modified from Dehaene & Cohen, 1995). The brain regions postulated for the three codes (M1-M3) are projected onto lateral views of the left (L) and right (R) hemispheres. Arrows represent theory-based assumptions about transcoding pathways between codes rather than empirically substantiated white matter tracts.

3.2. The neuroanatomical basis of TCM

The parietal lobes constitute the neuronal basis of arithmetic according to TCM (Dehaene & Cohen, 1995). Paralleling the theory-based distinctions between semantic and asemantic arithmetic processing, Dehaene et al. (2003) identified two sites within the parietal lobes with a partial hemispheric specialization, namely bilateral intraparietal sulci (IPS) and left angular gyrus (AG, see Fig. 1).

The bilateral IPS are suggested to represent an innate module for semantic magnitude processing (M1) in general, and right IPS is the site of the so-called mental number line (MNL, Dehaene, Piazza, Pinel, & Cohen, 2003). This is a conceived spatial representation of numbers on a logarithmic (typically in infants or kindergarteners, e.g. Opfer & Siegler, 2007) or linear (developing with age, e.g. Siegler, 2016) horizontal line following the place principle (ordinality, Rapin, 2016), usually from left to right in Western cultures (e.g. Kucian & von Aster, 2015).

In contrast to domain-specific magnitude-related processes located in bilateral IPS, left AG appears to be responsible for verbally mediated asemantic arithmetic fact retrieval (M2) in a domain-general manner (Dehaene et al., 2003). TCM originally postulated a left-hemispheric bias for M2, with recruitment of language-processing brain regions such as superior/middle temporal gyri (Dehaene & Cohen, 1995). Moreover, retrieval processes were postulated to rely on these verbal number representations as well as memory (Dehaene & Cohen, 1997). Subsequent lesion studies corroborated these assumptions (Dehaene et al., 2003).

The third TCM module for asemantic Arabic notations was postulated to be represented by a 'visual number form' (VNF, Cohen & Dehaene, 1991) located in the occipitotemporal gyrus of the ventral visual stream primarily of the left hemisphere with interconnections to a homologous right VNF (Dehaene & Cohen, 1995). It constitutes a specialized module for visually presented numerical input irrespective of cardinality and is associated with knowledge of the place principle underlying multidigit numbers (the so-called base-10-structure, Klein, Bahnmueller et al., 2013).

Dehaene and colleagues additionally outlined interactions of the core modules of number processing with other domain-general processes. Thus, executive functions such as choice of strategy and planning located in frontal cortices (Alvarez & Emory, 2006) were ascribed a supportive role during calculation (Dehaene & Cohen, 1997), and working memory functions are presumable mediators during calculation procedures (Dehaene, Molko, Cohen, & Wilson, 2004) in order to maintain intermediate results for subsequent recall e.g. during carry (in addition) or borrow (in subtraction) problems (Deschuyteneer, De Rammelaere, & Fias, 2005). Moreover, Dehaene et al. (2003) additionally found bilateral posterior superior parietal lobules (pSPL) to play a key role in domain-general processing of visuospatial attributes (Rapin, 2016). This structure has no direct theoretical equivalent in TCM in terms of a distinct module. Rather, visuospatial processes take the role of mediators between the asemantic Arabic number module (M3) and the magnitude representation module (M1, Dehaene et al., 2003). Accordingly, pSPL appears to enable orientation on the MNL (Krueger et al., 2011).

4. Results

4.1. Empirical evidence on TCM

4.1.1. Basic arithmetic operations and TCM

TCM predicts a double dissociation between simple arithmetic operations (Dehaene & Cohen, 1997). Whereas multiplication seems to rely on the verbally mediated retrieval of arithmetic facts from a memorized multiplication table (De Visscher & Noel, 2016), subtractions apparently require the abstract magnitude representation module (Zamarian et al., 2009; but see Holmes &

McGregor, 2007) independent of symbolic representation type (digits; words). Addition problems can either be solved verbally (like multiplication, Dehaene & Cohen, 1997) or with the help of the MNL represented by the magnitude module (like subtraction, Moll, Gobel, & Snowling, 2015). This leads to two basic hypotheses (see van Harskamp, Rudge, & Cipolotti, 2005):

First, TCM excludes a selective impairment of simple addition problems despite preserved multiplication and subtraction. Second, for the same reason multiplication and subtraction should not be impaired simultaneously when addition skills are preserved following TCM. Accordingly, there is rich evidence for double dissociations between multiplication and subtraction, including reports of isolated subtraction deficits (e.g. Lemer, Dehaene, Spelke, & Cohen, 2003) and of a selective impairment of multiplication (e.g. van Harskamp et al., 2005) in acalculic adults. A review of past neuroimaging studies on basic arithmetic confirms the dissociation between multiplication and subtraction (Zamarian et al., 2009). Empirical findings on division problems are less uniform. Apparently, a parsimonious approach is to redefine division operations as multiplication problems (in children; Robinson et al., 2006). Similarly, subtractions may also be solved using inversion, i.e. converting the problem into an addition operation as references (in adults; Campbell & Alberts, 2009).

The four basic arithmetic operations are also dissociable with respect to neuroanatomical representations. First, in adults (i.e. arithmetic expertise) a clear-cut distinction between subtraction and multiplication is reflected in operation-dependent activity in the bilateral IPS for subtraction on the one hand (e.g. Piazza, Pinel, Le Bihan, & Dehaene, 2007) and left-hemispheric AG (Delazer et al., 2003), supramarginal (Lee, 2000) or middle temporal gyrus (Prado et al., 2011) for multiplication on the other. Additions show a stronger dependency on the applied mental strategy. Simple addition (small numbers) may predominantly rely on asemantic retrieval-based strategies (Campbell, 2008) activating AG (like multiplication, Grabner, Ansari, Koschutnig, Reishofer, & Ebner, 2013; but see e.g. Rickard et al., 2000; Zago et al., 2001), whereas more complex addition tasks (large numbers) seem to require usage of the approximate number system activating IPS (like subtraction, Schmithorst & Brown, 2004). Note that this dichotomy is in line with the previously described behavioral predictions of TCM for addition problems, i.e. the strategy may either resemble subtraction or multiplication.

While these suggestions are well in line with TCM, converse findings challenge a strict separation between retrieval-based vs. magnitude-related processing as distinct problem solving strategies (Rosenberg-Lee, Chang, Young, Wu, & Menon, 2011). A systematic comparison between the neuronal networks involved in arithmetic (though omitting division) suggests only minor differences between the single operations (in children and adults; Kawashima et al., 2004), and previous operation-specific activation patterns may actually result from different task complexity levels at least in children (Rosenberg-Lee, Barth, & Menon, 2011), especially with regard to AG activity and developmental shifts in children (Chang, Rosenberg-Lee, Metcalfe, Chen, & Menon, 2015). These study results foster alternative accounts predicting overlapping activity between magnitude processing and fact retrieval (e.g. the abstract modular model, McCloskey, Caramazza, & Basili, 1985). However, another study indeed found operation-specific activity patterns for all four arithmetic subtypes in adults when controlling for task complexity (Fehr, Code, & Herrmann, 2007). That study also confirmed predictions of TCM with regard to task complexity effects: First, due to increased demands on domain-general processes including working memory and motor functions (representing finger counting according to Houde & Tzourio-Mazoyer, 2003), complex arithmetic activates frontal brain structures and motor systems irrespective of the specific arithmetic process (addition, subtraction etc., Dehaene & Cohen, 1995)

Second, following TCM complex arithmetic operations require enhanced magnitude processing independent of the specific arithmetic subtype (Dehaene & Cohen, 1995). Accordingly, there was a comprehensive cluster in right IPS conjunct over all four arithmetic operations in the high complexity condition in Fehr et al. (2007). Third, that IPS cluster was not visible for multiplication problems alone, corroborating the view that such problems are rather solved using fact retrieval strategies (as predicted by Dehaene & Cohen, 1995; see Zamarian et al., 2009 for a review). However, clusters in AG or pSPL were also lacking during multiplication. As the authors point out, activity in these regions was probably cancelled out in the applied complex vs. simple contrast due to equal demands on retrieval (AG) and spatial orientation on the MNL (pSPL) irrespective of complexity. Forth, multiplication problems showed additional activity in the left parahippocampal gyrus whose connectivity with frontal regions predicts success in arithmetic fact learning (Supekar et al., 2013). Hippocampal involvement in domain-general learning and fact retrieval is a central prediction of TCM (Moeller, Willmes, & Klein, 2015). And fifth, thalamic involvement was reported in the complex vs. simple contrasts for subtraction, multiplication, and division. This substantiates Dehaene and Cohen (1995, 1997) suggestion of a direct asemantic route for fact retrieval via corticothalamic connections during complex problem solving. The fact that it was not found during addition indicates a high degree of expertise for addition in general, leading to similar levels of thamalic activity during complex and simple problems (Fehr et al., 2007).

4.1.2. The neuroanatomical basis of TCM

As outlined above, TCM designates bilateral IPS as the center of magnitude processing (Dehaene et al., 2003). A vast amount of neuroimaging studies in adults demonstrate that IPS is sensitive to diverse manipulations of numerosity (Krueger et al., 2011; Wei, Chen, Yang, Zhang, & Zhou, 2014; see Cohen Kadosh, Lammertyn, & Izard, 2008 for a meta-analysis). Likewise, transient IPS lesions in adults initiated symptoms mimicking dyscalculia (Cohen Kadosh et al., 2007), and transcranial direct current stimulation of left IPS led to enhanced magnitude processing capabilities in a subtraction task (Hauser, Rotzer, Grabner, Merillat, & Jancke, 2013), further corroborating former claims of a lateralized specialization of IPS (Cappelletti, Lee, Freeman, & Price, 2010). However, deficits of split-brain patients with verbally mediated number comparison operations (activating the putative MNL) hint at right IPS involvement (Colvin, Funnell, & Gazzaniga, 2005), contrary to assumptions of TCM where verbally mediated arithmetic processing is restricted to the left hemisphere (Dehaene & Cohen, 1995). Such findings require a detailed explanation and may initiate modifications to TCM.

Besides numerical processing, IPS also nonspecifically responds to magnitude-related dimensions such as time (evidence from lesion patient and control; Cappelletti, Freeman, & Cipolotti, 2009) or space (Walsh, 2003). A key feature of the functional role of IPS may indeed be to represent the spatially aligned MNL (Dehaene et al., 2003; but see Doricchi, Guariglia, Gasparini, & Tomaiuolo, 2005 postulating frontal cortical involvement). Unanimous reports of IPS activity related to the spatial features of arithmetic operations support this view (e.g. Dehaene, Spelke, Pinel, Stanescu, & Tsivkin, 1999). TCM predicts that this spatial orientation on the MNL is conducted using pSPL, whose role may be to aid in transferring visually presented Arabic number information to the abstract magnitude representation module (Dehaene et al., 2003). Several neuroimaging study results in adults yield support for a relationship between pSPL activity and spatial numerical processing (Naccache & Dehaene, 2001; Pinel, Dehaene, Riviere, & LeBihan, 2001), and in children deficient mathematical competence goes along with reduced pSPL activity (Rykhlevskaia, Uddin, Kondos, & Menon, 2009), while MNL training leads to activation increases in pSPL (Kucian et al., 2011). Still, the MNL is apparently not automatically activated during number processing at least in adults (Zanolie & Pecher, 2014), contradicting a basic argument of TCM that needs clarification in future models. In adults, access to the MNL is apparently also required during carry operations ('semantic elaboration', Deschuyteneer et al., 2005), and this mandatorily involves access to the abstract magnitude representation (M1) represented by IPS and pSPL activity according to TCM. By contrast, fact retrieval is postulated for problems requiring no carry operation, as TCM postulates that the separate addition of tens and units suffices without accessing number magnitude. Therefore, TCM explains differences between problems with and without carries during additions in terms of distinct brain activity patterns. Thus, several studies on adults found activity in IPS during carries but AG involvement for problems free of carries (Klein et al., 2009; Stanescu-Cosson et al., 2000), and number magnitude manipulations only affected carry operations (Deschuyteneer et al., 2005).

Despite these occasional contradictions, there is a general consensus in the literature that right IPS is responsible for domain-specific magnitude processing (Henik, Leibovich, Naparstek, Diesendruck, & Rubinsten, 2012; but see Cohen Kadosh & Walsh, 2009 challenging the idea of an abstract magnitude representation), while left AG more likely processes domain-general arithmetic fact retrieval (M2 Dehaene et al., 2003). Accordingly, there are reports of left AG involvement in adults during trained multiplication (Delazer et al., 2003) and simple addition (Klein, Moeller, Glauche, Weiller, & Willmes, 2013) putatively reflecting retrieval-based operations, sometimes accompanied by left SMG activity (Lee, 2000; but see Rickard et al., 2000). Moreover, dyslexic children demonstrate impaired numerical fact retrieval skills, possibly caused by impaired phonological storage skills according to TCM (Simmons & Singleton, 2008). Thus, AG may assist in memory buildup by linking symbols and referents (Ansari, 2008).

Few studies systematically addressed the neuroanatomical plausibility of TCM as a whole. These report a high degree of overlap between empirically substantiated regions for arithmetic in adults (Anderson, Betts, Ferris, & Fincham, 2011;Schmithorst & Brown, 2004) and Dehaene and Cohen's (Dehaene & Cohen, 1995) anatomical outline. However, in one study right AG also responded to arithmetic manipulations (Anderson et al., 2011) in addition to left AG as predicted by TCM. Moreover, the fact that retrieval activates AG while magnitude processing involved IPS activity does not necessarily confirm basic claims of TCM. Thus, adult addition strategies were found to be primarily driven by circuitous counting procedures (activating IPS) even when the answer is stored in memory (reflected in AG activity in adults, see Fayol & Thevenot, 2012). It is therefore difficult to transfer an assumed underlying solution strategy to an observed brain activity pattern. After all, the association between AG and fact retrieval processing appears to be debatable. Accordingly, several lesion studies observed deficient retrieval skills in adults with spared AG (e.g. van Harskamp, Rudge, & Cipolotti, 2002; Zaunmuller et al., 2009). Besides, stimulating left AG did not affect familiarity processing (presumably reflecting fact retrieval) in a transcranial direct current stimulation study, promoting the idea that other brain regions may be involved (Artemenko, Moeller, Huber, & Klein, 2015). Furthermore, a previous study reported left AG activity not only during multiplication but also during subtraction in adults (Grabner et al., 2009) even though according to TCM subtraction engages magnitude processing (MNL).

Challenging TCM, Fayol and Thevenot (2012) suggest that all simple arithmetic operations require calculation procedures rather than retrieving of stored results, and that this process is reflected in AG activity. Price and Ansari (2011) alternatively advocate that left AG might be responsible for Arabic digit processing in general. This is in sharp contrast to TCM, which proposed that the corresponding M3 is represented by a specialized VNF (Cohen & Dehaene, 1991). Such a module dedicated solely to numbers has only recently been verified in the adult occipitotemporal cortex using intracranial recording (Shum et al., 2013), electroencephalography (Park, Chiang, Brannon, & Woldorff, 2014), and functional imaging (Grotheer, Herrmann, & Kovacs, 2016). A transcranial magnetic stimulation study further verified a genuine functional involvement of VNF in number processing (Grotheer, Ambrus, & Kovacs, 2016). Moreover, the postulated independence between phonological (M2) and visual Arabic (M3) numerical processing has also been confirmed based on distinct verbal digit to word conversion compared to quantitative digit to magnitude transcoding pathways in an aphasic patient (Dotan, Friedmann, & Dehaene, 2014). Indeed the latter may be deficient in DD (Rousselle & Noel, 2007).Still, there is ambiguity with regard to the lateralization of number processing in adults, some study results proposing a right-hemispheric bias (Park et al., 2014), whereas others found activity exclusively in the left hemisphere (see Arsalidou & Taylor, 2011 for a meta-analysis) or in both (Grotheer, Herrmann et al., 2016; Prado et al., 2011). Assumptions of TCM can directly account for contradictory left- or right-hemispheric activity in past studies: The model postulates that tasks requiring domain-general processes such as the verbally mediated retrieval of facts in memory should activate left-hemispheric language-processing regions, whereas tasks involving magnitude processing are more likely to lead to bilateral activity patterns (Dehaene & Cohen, 1995). In line with this suggestion, phonologically impaired alexia patients apparently demonstrate task-dependent arithmetic profiles: Operations depending on magnitude processing (addition, subtraction, and division) seem to be spared, whereas verbally mediated multiplication deficits were evident in a patient with pure alexia (Cohen & Dehaene, 2000).

In a study with minimized requirements on domain-general functions, right-hemispheric activation clusters were evident for presumable genuine number processing in adults (Park, Hebrank, Polk, & Park, 2012). The authors claim that interindividual variability in lateralization of basic number processing in VNF is contingent upon the degree to which IPS shows hemispheric specialization during arithmetic operations. Correspondingly, basic number processing (VNF) and arithmetic (IPS) show colateralization, i.e. similar degrees of lateralized activity in the same participants. This finding promoted the idea of an interindividually varying strength of functional (white matter) connections between parietal and visual cortices (Park et al., 2012). Such white matter tracts may in turn represent top-down control signals from IPS to VNF, suggesting that laterality effects are more likely or more pronounced in individuals with higher expertise in numerical processing (Park et al., 2012). Investigations of such white matter connectivity patterns lend additional support to TCM and are summarized below.

4.1.3. Connectivity between TCM codes

White matter tracts constitute communication routes in the brain (Kollias, 2012), either between homologous structures in the two hemispheres (commissural fibers), between regions within one hemisphere (association fibers) or from cortical to subcortical structures (projection fibers). TCM predicts several connections between the three postulated codes and other (domain-general) structures.

First, **intrahemispheric** transcoding paths were thought to interconnect all three modules in the left hemisphere, including independent semantic (M1 with M2 and M3) and asemantic (M2 with M3) routes (Dehaene & Cohen, 1995; Dehaene & Cohen, 1997). Meanwhile, for the right hemisphere, the authors postulated only semantic communication between M1 and M3 due to the lack of a verbal (asemantic) representation (M2, Dehaene & Cohen, 1995). Accordingly, association fibers are evident between VNF and left IPS in adults (Klein et al., 2016; Tang et al., 2006).Moreover, whereas connectivity between bilateral IPS and AG is also evident during healthy development, children with DD demonstrate hyperconnectivity (Rosenberg-Lee et al., 2015). In addition, there is empirical evidence that tracts between frontal and parietal cortices participate in arithmetic of adults (Klein, Moeller et al., 2013) as well as children (Rykhlevskaia et al., 2009), though there is as yet no consensus about the lateralization of these pathways (see Moeller et al., 2015 for a review). Interestingly, Klein et al. (2016) could disentangle dorsal as well as ventral white matter tracts connecting adults' AG to frontal cortices (during fact retrieval) from colocalized frontoparietal tracts (during magnitude processing; Klein et al., 2016). Such separate pathways are in line with basic assumptions of TCM. However, evidence on connections between VNF and AG is apparently still lacking, which may be due to a general focus of research on the magnitude vs. fact retrieval networks rather than to a lack of such a connection.

Second, TCM postulates **interhemispheric** (commissural) paths between the bilateral IPS (M1) as well as between the occipitotemporal areas (M3, Dehaene & Cohen, 1995) but not between both AG for phonological information (M2) due to the specialization of verbal information in the left-hemispheric (Dehaene & Cohen, 1995). In line with this suggestion, a reciprocal circuit between the bilateral IPS demonstrates strong effective connectivity during magnitude processing in adults (Krueger et al., 2011) as well as children (Cantlon et al., 2011;). The existence of such an indirect semantic route (i.e. one requiring the retrieval of the magnitude information from digits or number words) was further empirically fostered by demonstrating language-independent magnitude representation for approximate calculation after training of arithmetic facts which were originally linguistically mediated (Dehaene et al., 1999). Again, there is as yet no empirical evidence on the postulated route between the bilateral VFN.

Third, Dehaene and Cohen (1995) model also incorporates pathways between the three codes and **subcortical** structures such as thalamus or hippocampus (the latter being part of the direct asemantic route involved in fact retrieval without magnitude processing Dehaene et al., 1999). Indeed, Rykhlevskaia et al. (2009) identified projection fibers between thalamic nuclei and the corticostriatal tract in numerical cognition in children, and fibers connecting AG with the hippocampus were evident during fact retrieval in adults (Klein et al., 2016).

All in all, connectivity patterns in arithmetic provide insights regarding the development of arithmetic skills and the associated communication between the modules. In fact, longitudinal connectivity studies may even be useful to disentangle innate and acquired forms of arithmetic skills. Also, in future research they may prove helpful for the study of arithmetic acquisition and abnormal mathematical development.

4.2. Dyscalculia and TCM

4.2.1. Healthy development of arithmetic

The original version of TCM and subsequent extensions primarily relied on theoretical considerations derived from arithmetic deficits following neuropsychological or neurological impairments (e.g. aphasia or acalculia, Dehaene & Cohen, 1997) and imaging studies (Dehaene et al., 1999; Dehaene et al., 2003), i.e. from adults with matured neuronal circuits and arithmetic expertise. However, children differ from adults with respect to brain maturation and synaptogenesis (see Ardila & Rosselli, 2002 contrasting acalculia and dyscalculia), and this probably impacts on domain-specific abilities such as magnitude processing and on domain-general skills like working memory capacities (Kucian & von Aster, 2015). Indeed, whereas numerical processing predominantly elicits activity in bilateral IPS in adults, children mainly recruit frontal structures (Ansari, Garcia, Lucas, Hamon, & Dhital, 2005; Kaufmann et al., 2006). This hints at an ontogenetic specialization of IPS initiated by arithmetic education (Vogel, Goffin, & Ansari, 2015). A previous 'neuronal recycling' hypothesis (Dehaene & Cohen, 2007) accounts for such findings and postulates that structures originally responsible for magnitude in general (e.g. space, see Walsh, 2003) learn to execute numerical processing, especially with regard to orienting on the MNL (Dehaene 2005). This theory delivers a neuronal explanation for some well-established phenomena in number comparison tasks such as distance effects (increasing response times with decreasing distance between numbers, Hubbard, Piazza, Pinel, & Dehaene, 2005) or size effects (increasing response times with increasing magnitude of numbers, De Visscher & Noel, 2016) in terms of size-dependent precision levels of neuronal numbers representation (Dehaene, 2005).

Whereas the neural recycling model constitutes a theoretical approach, until now few models directly addressed the developmental aspects of numerical processing. An application of TCM to the development of numerical skills comes from von Aster and Shalev's 'four-stage model' (2007), where numerical expertise gradually develops from nonsymbolic subitizing, i.e. the innate ability to differentiate between small amounts of up to four discrete items (von Aster & Shalev, 2007) into an abstract representation (M1) with the associated principles of ordinality and cardinality. Symbolic magnitude – i.e. Arabic digits (M3) and subsequent fact retrieval (M2) – develop with arithmetic education. Fitting with this model is a shift from IPS to AG activity with growing expertise based on developmental changes in children (see Kaufmann, Kucian, & von Aster, 2014 for a review) and on training effects in adults (Zamarian et al., 2009). In the TCM terminology, such activity changes are consistent with increasing reliance on rote memory (M2) that develops as repeated calculation (M1) leads to associations between arithmetic problems and the respective solutions (Dehaene & Cohen, 1995; Dehaene & Cohen, 1997).

Findings from developmental studies open the opportunity to identify critical abilities and to integrate them into TCM. At present, several early predictors for children's math attainment are predominant in the literature: (a) visuospatial skills (Lauer & Lourenco, 2016; but see Butterworth, 2005) (b) MNL precision (Praet & Desoete, 2014; Reeve, Paul, & Butterworth, 2015; but see Muldoon, Towse, Simms, Perra, & Menzies, 2013), (c) innate number competence (Duncan et al., 2007; Jordan, Kaplan, Ramineni, & Locuniak, 2009), and (d) counting skills (Jordan, Kaplan, Locuniak, & Ramineni, 2007; Muldoon et al., 2013), all of which draw on M1 of TCM, and additionally (e) linguistic skills (Praet, Titeca, Ceulemans, & Desoete, 2013), which are represented by M2 for verbally mediated processes such as fact retrieval. Linking these findings with each other, mathematical education seems to go along with a transition from relying on magnitude-based (finger) counting to verbally mediated fact retrieval (Geary & Hoard, 2005). Likewise, low arithmetic competence in primary school is associated with immature finger counting strategies instead of automated fact retrieval (Jordan, Hanich, & Kaplan, 2003). On a neuronal level, this manifests in underdeveloped activity patterns, i.e. a recruitment of IPS that is not age-appropriate (De Smedt and Gilmore, 2011) and a concordant low AG activity (Grabner et al., 2007) in a DD sample compared to healthy controls. The reverse pattern is evident for trained vs. untrained arithmetic problems in healthy adults with a progressive replacement of IPS activity with AG recruitment (Delazer et al., 2003). Moreover arithmetic in healthy developing children elicits age-dependent shifts from primarily frontal clusters – presumably executing domain-general functions – to more dominant signal increases in IPS (Prado et al., 2011), pSPL (Cho et al., 2012; Rivera, Reiss, Eckert, & Menon, 2005), and AG (Prado et al., 2011), the latter possibly reflecting increased domain-specific processing.

4.2.2. Etiopathological concepts of DD and TCM

The previous findings are in line with the claim that anomalous IPS activity patterns observed in children with DD (De Smedt, Holloway, & Ansari, 2011; Molko et al., 2003) reflect an impaired domain-specific quantity code (Dehaene, Dehaene-Lambertz, & Cohen, 1998; Dehaene & Cohen, 2007). Thus, according to both the 'core deficit theory' (Wilson & Dehaene, 2007) and the 'defective module hypothesis' (Butterworth, 2005), individuals with DD suffer from impaired number processing due to a deficient number sense (M1). In line with this claim, children suffering from DD demonstrate reduced GM density in IPS (Rotzer et al., 2008). However, such conclusions can only be provisional as imaging studies allow a direct structure-function connection. Also, findings on IPS activity in DD are contradictory, and both stronger activity of IPS (Kaufmann et al., 2009; Kucian et al., 2011) as well as reduced IPS recruitment along with enhanced frontal activation (Mussolin et al., 2010; Price, Holloway, Rasanen, Vesterinen, & Ansari, 2007) may reflect compensatory mechanisms in DD (see Kaufmann et al., 2011 for a meta-analysis). Alternatively, Wilson and Dehaene (2007) suggest that the connection between IPS and other number processing regions is impaired rather than the quantity code per se, for which there is recent empirical evidence relating deficient white matter connectivity with abnormal mathematical development (in acalculia, Klein, Moeller, & Willmes, 2013; in DD, Kucian et al., 2014; see Moeller et al., 2015 for a meta-analysis). In a similar vein, the research groups of both Kucian et al. (2014) and Klein, Moeller, Willmes et al. (2013) independently formulated a 'dysconnection syndrome'/'disconnection hypothesis' account on DD and an analogous disconnection account exists for the possible cause of dyslexia (Richlan, 2012). A similar approach was followed in the 'access deficit hypothesis' (Rousselle & Noel, 2007), according to which children with DD have problems accessing the meaning of Arabic symbols, possibly caused by deficient connections between VNF (M3) and the magnitude module (M1).

So far, both prevailing alternative accounts on DD apparently fail to account for the deficit pattern observed in DD (Desoete, Ceulemans, De Weerdt, & Pieters, 2012; but see De Smedt and Gilmore, 2011 advocating a deficient access and Wong, Ho, & Tang, 2017 proposing a defective module). This may indicate that DD is not a unitary diagnosis but rather constitutes a collective category of math problems (Skagerlund & Traff, 2016) that evolve from congenital impairments in magnitude processing (defective module, Butterworth, 2005) or from a deficient skill to access symbolic (access deficit, Rousselle & Noel, 2007)

Other developmental accounts stress the importance of underdeveloped domain-general skills as a possible cause of arithmetic processing deficits in DD (Henik, Rubinsten, & Ashkenazi, 2011). For example, sustained attention is a good predictor of early numeracy competence (Steele, Karmiloff-Smith, Cornish, & Scerif, 2012), and children suffering from DD consistently demonstrate poor working memory capacities (Swanson, 2012) as well as visuospatial deficits (Geary & Hoard, 2005). Moreover, in line with arithmetic fact retrieval deficits in DD (De Smedt & Boets, 2010; De Visscher & Noel, 2016), children's phonemic awareness significantly mediates the impact of working memory on number transcoding (Lopes-Silva, Moura, Julio-Costa, Haase, & Wood, 2014). These findings suggest that poor domain-general skills may lead to alleged deficits of domain-specific abilities and could therefore contribute to the diverse DD symptoms. These considerations of interactions between domain-specific and domain-general factors may reconcile discrepant findings in the literature and should serve to encourage modified versions of TCM (see Hornung, Schiltz, Brunner, & Martin, 2014 for a similar idea).

In sum, our evaluation of developmental aspects of TCM is twofold. On the one hand, TCM cannot account for the existence of DD subtypes in its present form as it lacks specific assumptions about arithmetic development in children. First, developmental trajectories are not explicitly formulated for the model. Second, the multiple influences of domain-general factors before, during, and after initial arithmetic acquisition are not accounted for. This circumstance presents a gap, as different skills probably contribute to all of these phases, working both in concert with and being impinged by low-level domain-specific innate abilities in DD. On the other hand, TCM does account for discrepant findings in DD due to dissociations between operations – e.g. more reliance on rote memory for multiplication than subtraction (Zamarian et al., 2009) and within operations – e.g. more reliance on magnitude processing for approximate than exact calculation (Stanescu-Cosson et al., 2000).

4.3. Reasons for discrepant results

The studies included in this review vary greatly in many ways. As manifold arithmetic tests are required to analyze specific aspects of arithmetic processing, it is impossible to generalize across findings. In addition, many studies confound exact and approximate numerical processing because they involve qualitatively different task designs (Klein et al., 2009). For example, whereas easy tasks are often designed without carries, more demanding tasks typically involve carry operations. However, this probably leads to distinct requirements for domain-general skills such as working memory (Klein et al., 2009) and hence probably also to distinct neuronal activity patterns. As a consequence, it is impossible to argue that one region is inherently involved in one arithmetic operation but not in the other based on distinct studies. Indeed, already Dehaene and Cohen (1995) defined a hierarchy of four task complexity levels: First, fact retrieval is considered the simplest mode, followed by novel problems requiring recoding into simpler forms accessible to retrieval. Third, more demanding tasks are thought to involve domain-general skills such as working memory. And forth, some problems (especially multidigit operations) are postulated to require the use of strategies leading to higher demands on executive functions such as planning and control (Dehaene & Cohen, 1995).

Apart from methodological shortcomings, Kaufmann et al. (2013) identified varying diagnostic criteria as another potential confounding factor between studies so that DD samples are no comparable between studies. Unfortunately, it is common practice to pool over a heterogeneous group of children with atypical arithmetic test scores instead of defining discrete subgroups with distinct arithmetic patterns (Kaufmann et al., 2013). Moreover, hardly any of the studies included in this review included separate regressors for comorbid disorders which are common in DD (e.g. Butterworth & Kovas, 2013; Kucian & von Aster, 2015).

Finally, even healthy samples are not necessarily comparable, as they encompass a great age range covering all stages from infancy to adolescents to adulthood. As the postulated number sense is innate whereas arithmetic is an acquired skill that develops with education, the comparability between healthy samples is not assured.

4.4. Features of a comprehensive model of arithmetic development

TCM has become the ubiquitous model in the field of numerical processing. However, it lacks assumptions about presumable innate abilities such as subitizing and approximation (von Aster & Shalev, 2007) from which the adult magnitude representation (M1) supposedly develops (Rapin, 2016). Additionally, concrete assumptions about the pathways differentiating between developmental stages that young children must master are as yet outstanding. We suggest that comprehensive model of arithmetic development should address the following topics:

(a) Acquisition of arithmetic knowledge: How and when does arithmetic develop? What factors are required for arithmetic expertise?
(b) Characterization of intermediate stages of arithmetic expertise: Are there critical stages in young children? How can training and education help in mastering the respective requirements?
(c) Magnitude vs. fact retrieval: Is intact magnitude processing a precondition for arithmetic rote memory? At what stage (storage or retrieval or both) does it influence rote memory? Are there differences between children and adults? Which is affected in DD?
(d) Significance of motor functions in arithmetic: Is finger counting an intermediate (immature) arithmetic strategy or does it prevail in adult counting? How may it help in arithmetic education? Is finger counting an efficient therapeutic tool in DD?
(e) Role of domain-general skills in acquisition and consolidation of mathematical knowledge: Are deficits in supportive functions (e.g. WM) causally involved in low achieving mathematicians? At what developmental stage are such functions particularly influential? Can training programs help to mitigate or prevent abnormal mathematical development?
(f) Connectivity between parietal, frontal, and subcortical brain areas in children's acquisition of arithmetic expertise: Does the disconnection account of DD apply to abnormal mathematical development? How do connectivity patterns differ between healthy children and children with DD? Which connections among the TCM codes are primarily affected?
(g) Innate vs. educational aspects of VNF: When does VNF specialize in number processing? Are there precursors for abnormal mathematical development in young children's number processing systems? Can number training improve VNF formation especially in DD?
(h) Neuroplasticity of arithmetic expertise: How do brain activity patterns mature during the acquisition of mathematic expertise?

Additionally, the apparent lack of direct assumptions about DD and numerical development should be addressed in the future in models of numerical development. In recent years, some research groups have started to outline such models (Kaufmann et al., 2011; von Aster & Shalev, 2007), but longitudinal evaluation studies are still lacking, and so is a detailed empirical depiction of precursors for successful arithmetic acquisition. Thus, impaired counting, fact retrieval, and computation strategies are key features of DD (Jordan et al., 2009) and should be accounted for using a developmental perspective. Identifying precursors and their deviations in DD will also help to refine DD diagnostic criteria with regard to DD subtypes (Karagiannakis, Baccaglini-Frank, & Papadatos, 2014) in order to increase diagnostic sensitivity and specificity.

4.5. Outlook

Since TCM was first outlined in the late 1990's, there has been major progress in terms of methodology (e.g. brain imaging), developmental studies (cross-sectional; longitudinal) as well as diagnostics. Therefore, some of the initial statements were elaborated on, others revised and some rejected. Nevertheless, the main scaffold of this multiroute model still shapes the majority of arithmetic theories, and findings in various fields of arithmetic research today are frequently integrated into the framework of TCM. From this intermediate stage, the next step should be to model arithmetic development and the associated developmental deviations and to subject the resulting models to an empirical evaluation.

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