Neurocognitive components of mathematical skills and dyscalculia

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Abstract

The search for the cognitive determinants of mathematical skill has a long history. For some time it has been thought that mathematical proficiency is not determined by a single unique underlying cognitive factor but by multiple cognitive components such as memory, spatial processing or executive function. Yet it remains unclear exactly what these cognitive components are and how it is that they have an impact on mathematical skills. I argue that specific neurocognitive explanatory models of cognitive components promise to increase our understanding of how cognitive components play a role in numerical and mathematical tasks and determine performance. I outline how recent advances in the understanding of the neurocognitive mechanisms of sensory processing, working memory and executive functions lead to meaningful hypotheses about their functional involvement in mathematical performance. I also touch upon how this might shed light on dyscalculia and its comorbidity with other learning deficits.

Keywords: mathematical cognition, mental arithmetic, dyscalculia, brain imaging, working memory, spatial attention, executive functions, performance adaptation, spatial cognition, serial position

The search for the cognitive systems that support mathematical skills has a long history. It has long been thought that mathematical proficiency is determined by multiple cognitive components (e.g., Geary, 1993), comprising both cognitive functions (such working memory) and mental representations (such as multiplication facts stored in memory). Some influential accounts emphasized cognitive functions, whereas others highlighted the representations. Geary (1993), for instance, proposed working memory to be a crucial factor explaining individual differences in math achievement. Dehaene (1992) specified a cognitive model that was based on three crucial types of representation: verbal, Arabic and analog, each being the core code for specific numerical abilities: the verbal code for arithmetic tables, the Arabic code for multi-digit operations and the magnitude code for approximate calculation.

With the advent of neuroimaging techniques, attention has shifted away from this multiple component approach toward he search for quantity representation as the central determinant of math skill and dyscalculia. With brain imaging studies revealing consistent activation associated with experimental manipulation of quantity, the intraparietal sulcus (IPS), and in particular its more anterior regions forming the horizontal segment, has been taken as the brain region at the core of mathematical processing, the efficiency of which determines math skill (Butterworth, Varma & Laurillard, 2011; Dehaene, Molko, Cohen & Wilson, 2004). This view has been strengthened by demonstrations that this area is processing numerical magnitude in young children, as shown with functional magnetic resonance imaging (fMRI) in 4-year old children (Cantlon, Brannon, Carter & Pelphrey, 2006) and with EEG (Izard, Dehaene-Lambertz & Dehaene, 2008) and functional Near Infrared Spectroscopy (fNIRS, a brain imaging technique that measures brain activity in the outer surface of the brain based on the amount of absorption of near-infrared light that is emitted to the brain) in children of a few months old (Hyde, Boas, Blair & Carey, 2010). Moreover the fact that many animal species show the same behavioral characteristics as humans when processing quantity and that neurons in the homologue intraparietal areas of the macaque code numerical magnitude in a way that is compatible with the behavioral characteristics (Nieder & Miller, 2004; for reviews see Geary, Berch, & Mann Koepke, 2015), has been taken as strong evidence that the quantity representing neural system situated in the intraparietal sulci constitutes the phylogenetic precursors of formal mathematical competencies. Of course, in animals and in preverbal infants these representations are approximate rather than exact. That is why this system is often referred to as the approximate number system (ANS). The proposal that the ANS is the biologically based center of our intuitive understanding of number is strengthened by genetic studies showing that the contribution of parietal areas to mathematical tasks is heritable (Pinel & Dehaene, 2013) and that genetic diseases that are associated with math problems are accompanied by structural and functional impairments of the parietal areas (Molko, Cachia, Rivière, Mangin, Bruandet, Le Bihan & Dehaene, 2003). It has also been taken as an ontogenetic starting point for the development of more complex and schooling-induced formal arithmetic. It has been proposed that an impaired or inaccurate quantity representation system is taken to be the most important determinant of math skill and the core deficit of developmental dyscalculia. For instance, Halberda, et al. (2008) found that the precision with which the quantity of two sets of dots can be compared correlates retrospectively with scores on standardized math tests, but the strength of this relation is currently debated (Chen & Li, 2014; De Smedt, Noël, Gilmore, & Ansari, 2013; Fazio, Bailey, Thompson & Siegler, 2014).

An important question that can be raised is how a single factor like the ANS can be reconciled with the multifaceted nature of mathematical cognition and with the heterogeneity of developmental dyscalculia. Indeed, the major picture that emerges from the literature is that developmental dyscalculia is associated with many more cognitive deficits, is relatively heterogeneous and often co-occurs with other developmental disorders. Although the exact numbers vary largely from study to study, it is clear that comorbidity of dyscalculia with dyslexia, ADHD, developmental dyspraxia among other common childhood disorders is not exceptional (Shalev, Auerbach, Manor & Gross-Tsur, 2000). Critically, brain imaging studies also suggest multiple brain areas are recruited during the solving of mathematics problems. In addition to the ANS in the IPS, multiple areas are engaged even during the solving of numerical problems that are thought to directly tap the ANS, such as number comparison (Arsalidou & Taylor, 2011; Fias, Menon & Szucs, 2013). Although the activations obtained with brain imaging are merely correlational with cognitive activity and although clear relations with math skill have not always been reported, the involvement of a broad set of brain regions suggests a more complex picture than that implied by the ANS theory.

Demonstrating that number processing is subserved by multiple brain regions is an important first step, but in itself it leaves the functional specification of cognitive components unexplained. What is needed are neurocognitive theories that describe in detail the representations and processes that subserve arithmetic tasks and how they are implemented in neural systems. Such knowledge is needed to come to a deeper understanding of what determines math skill and difficulty. Below, I review some of the neurocognitive components that have been documented to be strongly related to number processing and are therefore plausible sources of variability in mathematical achievement.

1. Accessing quantity representations

Single cell recordings in the IPS of macaque monkeys (Macaca mulata) while they view dot displays of varying numerosity have established the precise characteristics of how quantity is neurally encoded. The most important property of these neurons is that they are tuned to a specific number (Nieder & Miller, 2004). This property is called number selectivity and means that the neurons have a preferred number and respond maximally when their favorite numerosity is displayed (e.g. 3 dots). The neural response decreases as a function of the numerical distance between the number displayed (hence a weaker response for 2 and 4 compared to 3 and an even weaker response to 1 and 5). Using the technique of fMRI adaptation, Piazza, Izard, Pinel, Le Bihan & Dehaene (2004) were able to demonstrate that the same property characterizes the neural coding of number in the IPS of human adults, with a more precise tuning for symbolic numerals (e.g. '5', '8') than for number presented non-symbolically as collections of dots (Piazza, Pinel, Le Bihan & Dehaene, 2007).

The question that directly follows is how sensory input that conveys numerical information, either in non-symbolic format or as number symbols (like digits or number words) is transmitted to the number-selective coding in IPS. In other words, what type of preprocessing is needed to transform sensory input to access the parietal quantity representations. We initially addressed this question with computational modeling (Verguts & Fias, 2004).

Our starting point was that the transformation of neural activity in retinotopic visual areas induced by a collection of dots into a number-selective neural code is non-linear. More concretely, when two dots are presented, then the neuron with the preference for 2 should respond, but when another dot is added, then the number 2 neuron should not respond, but rather the number 3 neuron should respond. Consequently, a direct coupling between sensory input and number-selective neurons is not a sufficient explanation. A computationally plausible way to accomplish such non-linear transformation is to have an intermediate layer. We built an artificial network that comprised an additional layer of neurons between an input layer and an output layer. We used the back propagation learning algorithm (Rumelhart & McClelland, 1986) and we trained the network to give appropriate number-selective responses. After learning, the intermediate layer had learned to summate or accumulate the number of objects that were presented at input. More concretely, with more objects presented, more neurons became active. Based on this work, we hypothesized that for non-symbolic quantities, the number-selective neurons in IPS can only be a accessed via a preprocessing stage that converts visual input into an accumulation code, which is sensitive to number, but is not number-selective.

The biological reality of this hypothesis was later confirmed by the observation that neurons in the lateral intraparietal area of the macaque monkey followed the principles of accumulation coding (Roitman, Brannon & Platt, 2007). This observation was further supported with a series of human fMRI studies demonstrating a pattern of brain activity that is consistent with the hypothesis of accumulation coding (Santens, Roggeman, Fias & Verguts, 2010). A region of the parietal cortex that is functionally equivalent to the lateral intraparietal area of the monkey, but in humans located more medially, showed increasing activation with visual displays containing more dots. It was also shown that this region was more important during the processing of non-symbolic numerosities compared to the processing of Arabic numerals, which is consistent with the model, as mapping symbols to number-selective neurons can be done directly and does not require preprocessing. We also demonstrated that, although accumulative activity in this region has been shown to be limited to 4 elements in visual short-term memory tasks (Todd & Marois, 2004), accumulation does not level off at four elements in the context of a task requiring enumeration (Knops, Piazza, Sengupta, Eger & Melcher, 2014; Roggeman, Fias & Verguts, 2010). To situate accumulation coding and number-selective coding with respect to each other, my colleagues and I performed an fMRI adaptation study, in which we could show that the processing stream from visual input, via number-sensitive to number-selective processing follows a posterior to anterior gradient along the dorsal visual processing stream, which runs from occipital to parietal cortex (See Figure 1; Roggeman, Santens, Fias & Verguts, 2011).

It is clear that considerable processes precede the seemingly simple translation of dot displays into number-related neural codes. Although there is no direct evidence that explicitly supports this, it can reasonably be predicted that the integrity and quality of the accumulation system and by extension of the whole dorsal stream (i.e. visual information that is processed from occipital to parietal cortex) is a prerequisite for an efficiently functioning number-selective processing system. As the number-selective processing system forms the neural implementation of the ANS, this would imply that not only the number representation itself but also the mechanisms that provide access to it can potentially contribute to mathematics learning. It is not difficult to imagine that impoverished preprocessing may, through development, lead to an ANS low in precision.

Despite the fact that converting symbolic numbers (i.e. in Arabic or verbal format) into a number-selective neural code is less complicated, in the sense that it is a linearly separable problem, the pathways that are followed also need to be intact for normal development. The precise mechanisms of the numeral to number-selective coding pathway are not fully understood, but evidence is accumulating that an inferior temporal region in the ventral stream of the right hemisphere is involved (Shum, Hermes, Foster, Dastjerdi, et al., 2013). The precise properties of this visual number form area are not yet described. Crucially, the Arabic number system is a base-ten positional system in which numeral position determines the associated quantity (e.g., the 4 in 43 represents 40, but 4 in 34). Hence, determining position-specific digit identity is essential, thus structurally resembling - at least partially - the coding of position of letters in word reading. It might therefore be very revealing to explore to what extent the visual number form area (in the right hemisphere) and the visual word form area (in the left hemisphere) have common processing characteristics and to what extent they differ from each other. This information might open a window to understand how and why developmental dyscalculia regularly co-occurs with developmental dyslexia (Shalev et al., 2000). It also might constitute a more detailed functional elaboration of the idea that developmental dyscalculia, as expressed in poor ANS representations, might be attributed to initial deficiencies in mapping numerals to number magnitude (Noël & Rousselle, 2011; Rousselle & Noël, 2007; vanMarle, Chu, Li, & Geary, 2014).

2. Working memory: the role of serial order

Of course, number processing as it occurs in arithmetic or math consists of more than coding the numerical magnitude value of a numeral. It requires relating different numerals to each other, possibly producing new ones, as when computing the sum of two numbers. This requires a working memory that permits relevant numbers to be kept in mind, relating them to each other, and performing operations on them (Bull & Lee, 2014). This is confirmed by studies showing that occupying working memory resources in dual-task situations may impair number processing tasks. This is true for verbal as well as for visuo-spatial working memory, depending on the task (see Raghubar, Barnes & Hecht, 2010). Also correlational approaches reveal a link between working memory and numerical task performance as well as general math skill (for a review, see Geary, 1993). Furthermore, brain imaging evidence shows that brain activity in the IPS during a working memory task is predictive of arithmetical performance two years later (Dumontheil & Klingberg, 2012).

Working memory is a cognitive function that consists of several subcomponents. Of course, an important overall distinction is between verbal working memory operating via a phonological loop and visuospatial working memory operating as a visuospatial sketchpad (Baddeley, 1986). The differential contributions of these two working memory modalities to mathematical processing have been described to some extent, with verbal working memory contributing more to rote verbal memory retrieval as in table-based multiplication and visuospatial working memory contributing more to strategy-based calculation as in column-wise addition (Imbo, Vandierendonck & De Rammelaere, 2007). Yet, there are other basic subcomponents to be distinguished. A first distinction that can be made is between item memory and order memory. Both aspects of information are important for efficient working memory and are based on distinct neural circuits (Majerus, D'Argembeau, Martinez Perez, Belayachi, et al, 2010). Second, storage and operation are seldom distinguished in their relation to mathematical achievement. Overall, the specific relationships of these subcomponents of working memory with math skill have not been explored. Typically, investigations of working memory involvement in math skill are confined to relating capacity as a relatively global measure of working memory function to performance. Yet, there is reason to believe that the link between working memory and number processing can be described at a more refined functional level. I will focus on order working memory and attentional mechanisms in working memory respectively to illustrate this point.

2.1. Number processing shares neural resources with working memory

At a behavioral level, there is a close resemblance between processing the ordinal aspects of number (which is the larger number?) and the ordinal aspects of information that is maintained in working memory (which of the two items was further in the working memory sequence?). An important factor driving performance in both number comparison and working memory order judgments is the distance effect. It is more difficult to determine which of two numbers is the larger the closer the numbers in terms of magnitude of the numbers. Similarly, the closer two items are in working memory, the more difficult it is to determine which of the two items is positioned before (or after) the other (Marshuetz, 2005). In addition, Marshuetz et al.'s (2000) early brain imaging study of adults showed that judgments about serial order in working memory (Remember z-t-g-p-l. Are t-g in the correct order?) but not identity judgments (Did t belong to the working memory sequence?) recruit areas in the bilateral IPS similar to those activated in number processing.

In a study that used the same type of order and item judgment tasks, Majerus et al. (2010) went one step further. They presented either sequences of faces or of nonwords and engaged participants in an order judgment task or an item judgment task. It was discovered that the IPS of the right hemisphere was involved in order judgments with both types of stimuli, suggesting that the neural coding of serial position in working memory occurs at least partially in a modality-independent way. Modality-specific effects were observed for face stimuli in the right fusiform area and for letter strings in the left hemisphere language processing areas. These results suggest that working memory emerges from the use of modality-independent ordering processes geared toward sensory networks that underlie the processing and storage of modality-specific item information. The fact that the intraparietal sulci are involved in processing order in a stimulus-independent fashion is further corroborated by a study that investigated to extent to which the processing of numerical and of alphabetical order recruit the same brain areas. This study revealed that the brain activations induced by a number comparison task (which of two numbers is the largest?) and by an alphabet position comparison task (which of two letters is the furthest in the alphabet?) overlapped in a number of brain areas comprising the intraparietal sulci and premotor cortices (Fias, Lammertyn, Caessens & Orban, 2007), which are highly similar to those brain areas that are active in the serial order working memory tasks as described above.

Although suggestive of overlapping neural circuitry for the processing of order as expressed by numbers, letters, or position in working memory, these studies by themselves are not conclusive. Indeed, because of the fact that there are thousands of voxels in the brain and for methodological and statistical reasons, it is impossible to determine an overlap purely de visu. What is needed is a demonstration of the very same voxels being active in the different task contexts, in the very same subject and in the very same scanning session. That is exactly what Attout, Fias, Salmon & Majerus (2014) aimed to do. They searched for the neural correlates of the distance effect as it was observed in three tasks addressing order: a number comparison task (is this number larger than 65?), an alphabet position task (are the two letters in alphabetic order?) and a working memory order task (do the two letters occur in the same order as you have just learned them?). It was found that the activity in the horizontal segment of the left IPS reflected the distance effect in all three tasks. The corresponding area in the right hemisphere was jointly activated by the number and working memory task, although it was not activated in the alphabetic task. Also in some superior frontal areas that are typically observed in working memory tasks, a overlapping activations between the three tasks were observed.

Hence, generally speaking, brain imaging studies strongly suggest that the neural circuitry that is used to process numerals is strongly related to the processing of serial order in working memory. It is not clear at this point, however, which common operational mechanism is expressed in this overlapping neural circuitry. There are a several possibilities that one can consider. First, it is possible that somehow numbers are used to provide the serial position code of working memory. This can be done in a more or less explicit way as when using counting to tag items in working memory (Noël, 2009). However, it is also possible that the link is not made via procedural aspects of counting. Instead it may be that it are the representational characteristics of the number-selective neural system itself that are important. Botvinick and Watanabe (2007) showed that a computational model of working memory in which ordinal rank was coded with the same properties as number-selective neurons is able to predict behavioral serial position effects in working memory in great detail. Second, it is also meaningful to consider the possibility that a number is not processed in isolation but always in the context of other numbers, whereby working memory provides this context. By placing numbers in working memory together with other numbers and by doing this in a systematic way, numbers may acquire their functional meaning. A straightforward prediction of this idea is that number processing is to a large extent context dependent. One of the cases where a strong context dependency is observed is the relationship between number magnitude and space. That is what will be discussed in the next section.

2.2. Serial position in working memory links numbers to space

The representation and processing of number is tightly connected to the representation and processing of space. This is typically interpreted as an expression of the fact that numbers are represented as positions on a spatial mental number line typically running from left to right in left-to-right reading cultures and vice versa in right-to-left reading cultures (Dehaene, Bossini & Giraux, 1993).

One of the most important pieces of evidence in support of this link between number and space comes from the SNARC effect, which is an acronym for Spatial Numerical Association of Response Codes (Dehaene et al., 1993). It reflects faster left hand than right hand responses for small numbers and faster right hand than left hand responses for large numbers, expressing a clear association between small numbers and left and large numbers and right. In right-to-left reading cultures, these associations are reversed (Shaki & Fischer, 2008; Zebian, 2005;). The SNARC effect isn't confined to one particular task, but has been observed in parity (odd-even) judgment, magnitude comparison, and even in tasks that don't require processing of the number semantics at all, such as indicating whether a number is presented in italics or not, or even when a number is presented merely as a background against which shapes are presented and the shapes have to be responded to (Fias, Lauwereyns & Lammertyn, 2001). This suggests a high degree of automatic processing of number magnitude and its relation to space.

The SNARC effect is commonly interpreted as an expression of the fact that a number's magnitude is represented as a position on an oriented number line in memory (see Hubbard, Piazza, Pinel, & Dehaene, 2005). Yet, a number of observations suggest that the associations between number and space are more flexible than would be expected from a long-term memory representation. First, the SNARC effect is range dependent. Dehaene et al. (1993) and Fias, Brysbaert, Geypens & Ydewalle (1996) showed that numbers 4 and 5 were preferentially responded to with the right hand when they were represented in the context of small numbers (i.e. the range from 0 to 5). However, when the same numbers were presented in the context of larger numbers (i.e. the range from 4 to 9), the numbers 4 and 5 showed faster left than right hand responses. So apparently, it is not long term absolute numerical magnitude that drives the SNARC effect but rather the number's magnitude relative to the context in which it occurs. Second, it has been shown that the SNARC effect depends on visual imagery (Bächtold, Baumüller & Brugger,1998). When participants are asked to imagine number stimuli as being placed on a ruler a typical SNARC effect is observed. Yet, when participants are instructed to imagine numbers as being positioned on a clock face, the SNARC effect reverses, with the small numbers associated to right and the large numbers associated with left, which is consistent with how numbers appear on a clock. Third, the SNARC effect has been shown to be flexibly dependent on reading habits (Shaki & Fischer, 2008). When Russian - Hebrew bilinguals had read a Russian text just before the SNARC effect was measured, a normal SNARC effect was observed, but after having read a Hebrew text, which is read from right to left, the SNARC effect was reversed. All these observations indicate that spatial coding is not inherently associated to number but that it is constructed during task execution, suggesting a crucial role of working memory.

A straightforward way to test the involvement of working memory is to use a dual-task design in which one task occupies working memory resources and then measure the SNARC effect while executing the main number processing task. Herrera, Macizo & Semenza (2008) used this approach with a visuospatial working memory load and found that the SNARC effect in a number comparison task was abolished. van Dijck, Gevers & Fias (2009) extended this approach by adding a condition in which verbal working memory was loaded by asking participants to keep a string of consonants in memory and by including a parity judgment task. It was observed that working memory load indeed abolished the SNARC effect in the two tasks but that it occurred in a modality-dependent fashion. The parity judgment SNARC effect was abolished by a verbal working memory load but not by a visuospatial working memory load, the opposite being the case for the number comparison task.

The necessity of having working memory resources available for the SNARC effect to occur raises an important question: Which aspect of working memory processing determines the SNARC effect? As was highlighted above, working memory order tasks and number processing tasks share neural resources, hence a plausible candidate is the processing and representation of serial position (Fias, van Dijck & Gevers, 2011). One possibility is that it is serial position in working memory rather than number magnitude itself that is related to space. This can explain the SNARC effect if one makes the additional assumption that while executing a number task working memory is invoked to temporary store number stimuli and their responses as part of the task set to facilitate and to optimize task performance (Monsell, 2003). Storing numbers in working memory as a function of magnitude is a very efficient way to fully exploit the limited working memory resources as it allows chunking (rather than having one number in each available slot, one can organize numbers in chunks [e.g. 1-2, 3-4, 5-6 etc.] and then allocate a chunk to a slot) and as it facilitates efficient access to specific numbers (e.g. if you have located 4 then you know that 5 is next to it).

To test the hypothesis that serial order in working memory is spatially coded and to determine whether this drives the SNARC effect, van Dijck and Fias (2011) designed the following experimental procedure. Participants were asked to encode and remember a sequence of numbers that was ordered arbitrarily (e.g. 6-3-1-9-8-4). During the retention interval numbers were presented and participants had to perform a parity judgment task, but only if the presented number was part of the memory list. This latter restriction was imposed to make sure that participants accessed working memory to solve the task. Thereafter a recognition task was administered to verify whether the participants had correctly memorized the sequence. This cycle (encoding, parity judgment during retention interval and then recognition task) was then repeated each time with a different list of to-be-remembered numbers. With this design it is possible to separate numerical magnitude from serial order in working memory and thus to determine whether the left or right hand response times were modulated by serial position in working memory and/or numerical magnitude. It was clearly found that serial position in working memory was associated to space with initial items receiving faster left hand response than right hand responses, the opposite being true for items towards the end of the memory sequence. Number magnitude by itself was not systematically associated to the side of response.

To take this idea one step further, it was reasoned that the generator of the SNARC effect is not specifically number related and therefore does not have anything to do with numbers as such and that therefore the same effect can be obtained with whatever information is stored in working memory. This was tested in a follow-up experiment in which it were not sequences of numbers that were stored in working memory but rather fruit and vegetable names. And a fruit/vegetable categorization task was administered instead of a parity judgment task. Again an association was found between position in the sequence and space, with initial items associated with left and end items associated with right. Interestingly, the same participants were subsequently administered a classic parity judgment task to measure their conventional SNARC effect. It was found that the size of the position-space association correlated significantly with the size of the SNARC effect, corroborating the hypothesis that it is serial position in working memory that drives the SNARC effect.

In sum, the temporary position-space associations are what drive the SNARC effect, rather than the long-term semantic representations of number to which the SNARC effect is traditionally ascribed. This provides a natural explanation for the fact that the SNARC effect has been shown to be flexibly dependent on the range of numbers used, on reading habits and on visual imagery, as well as for the fact that the SNARC effect has also been demonstrated with non-numerical ordinal information like letters, days of the week or months of the year (Gevers, Reynvoet & Fias, 2003; Gevers, Reynvoet & Fias, 2004). It is suggested that efficient number processing does not merely entail retrieving the correct semantic information and corresponding responses, but that it mobilizes working memory resources to create a mental workspace in which information is systematically ordered to facilitate performance.

2.3. Workspace engages spatial attention

Number processing has been shown to engage mechanisms of spatial attention, the original idea being that spatial attention is used to move back and forth along the mental number line. The main sources of evidence are twofold. First, Fischer, Castel, Dodd & Pratt (2003) used a variant of the Posner cueing paradigm. In this paradigm a spatial cue is typically presented that directs attention to the left or the right. If a target is presented at the cued location, then target detection is facilitated. In Fischer et al.'s variant, a numeral was presented centrally as the cue. It was found that a small number cue facilitated detection of a left target and that a large number cue facilitated right target detection. Second, Zorzi, Priftis & Umiltà (2002) examined left hemineglect patients' performance on a number bisection task. After brain damage to the right hemisphere, left hemineglect patients ignore the left side of visual space. This is truly an attentional deficit and is not caused by problems at the level of sensory input. As a consequence of their attentional bias, patients exhibit behaviors like eating only the right side of their plate or shaving the right but not the left side of their face. In more formal tests, neglect patients show a rightward bias in a line bisection task: when asked to mark the midpoint of a line, patients deviate toward the right since they ignore the left side of the line. Analogous to this, Zorzi et al. (2002) asked left neglect patients which number is the midpoint between two other numbers. The patients produced answers that systematically deviated toward larger numbers. So, for instance, when asked which number is the midpoint between 1 and 9, neglect patients say 6 or 7 rather than the correct number 5. Importantly, this occurs in the absence of problems in mental arithmetic. Hence, patients have no difficulty computing the correct result of problems like (1+9)/2, excluding the possibility that their number bisection error is due to an impaired capacity for mental arithmetic.

Recall the theoretical proposal that the link between numbers and space is not so much attributable to the properties of the long term representation of number magnitude taking the form of a spatially oriented mental number line, but rather to the involvement of working memory to serially order numbers as a function of task requirements. Therefore one can wonder to what extent the number cueing paradigm and the number bisection task in neglect derive from spatial attention mechanisms that operate in the workspace in which serial position is spatially coded.

To test whether spatial attention operates in working memory, van Dijck, Abrahamse, Majerus & Fias (2013) embedded the cueing paradigm of Fischer et al. (2003) in a working memory context. Participants first had to memorize a list of numbers in arbitrary order and during the retention interval they had to detect a left or right appearing target that was preceded by a number cue, only having to respond when the number belonged to the list they maintained in working memory (see Figure 2). The results show a cueing effect, not on the basis of the numerical magnitude of the number, but of the position of the number in the memorized list: with a cue from the beginning of the list, left targets were detected faster and with a cue from the end of the list, right targets were detected faster. This was the case, irrespective of whether participants indicated target detection by a manual or a vocal response and was also replicated in some modified versions of this paradigm (for an overview see Abrahamse, van Dijck, Majerus & Fias, 2014). The effect is strong and robust, in contrast to the original Fischer et al. study which has been proven to be difficult to replicate (Zanolie & Pecher, 2014). It is highly likely that the reason that the effect is weak in the original paradigm is due to the fact that encoding in working memory was not required for task performance and that therefore subjects may not have consistently stored numbers in working memory spontaneously (van Dijck, Abrahamse, Acar, Ketels & Fias, 2014).

As far as the number bisection bias in neglect patients is concerned, there are also indications that working memory is involved. First, it has been shown that the bisection bias with lines does not correlate with the bisection bias observed with numbers (Rossetti, Jacquin-Courtois, Aiello, Ishihara, Brozzoli & Doricchi, 2011). Even more importantly, the number bisection bias was only observed in patients whose lesion extended more anteriorly in frontal areas and whose working memory capacity was affected (Doricchi, Guariglia, Gasparini & Tomaiuolo, 2005). Second, van Dijck, Gevers, Lafosse, Doricchi & Fias (2011) reported on a single case who showed right spatial neglect after left hemisphere lesion as evidenced by a bias towards the left in a line bisection task. Surprisingly, however, this patient did not present a bias toward smaller numbers in the number bisection task as expected, but a bias towards larger numbers. Her SNARC effect was normal with small numbers associated with left and large numbers with right, indicating that her number-space associations were not reversed as they should have been if numbers are spatially arrayed on a mental number line. Further investigations of her working memory showed that she had pronounced problems with initial items of verbal sequences encoded in working memory, which is consistent with the direction of her number bisection bias. Of course, this is only a single case and it is difficult to judge at this point to what extent the involvement of a specific working memory deficit accounts for the pattern of number bisection bias in neglect patients. A study involving multiple cases shows that a working memory deficit is not the determining factor in all cases (Storer & Demeyere, 2014), but that study does not exclude the possibility that number bisection bias can be determined by multiple factors of which working memory is one (e.g. van Dijck, Gevers, Lafosse & Fias, 2012).

In sum, it is clear that number processing, spatial attention and working memory are tightly interwoven. Moreover, they recruit common brain areas, in particular the intraparietal sulci. A crucial question, then, is to what extent this configuration of rather basic processes is a determining factor of mathematical skill. In a study that investigated number processing in a group of children with visuospatial disabilities, Bachot, Gevers, Fias & Roeyers (2005) found that children (aged 7 to 12) with a small visuospatial working memory capacity and poor performance on number concept (e.g. 12 is 9 apples more than?) and complex addition tasks (26+63=) also exhibited a reduced SNARC effect in a number comparison task, compared to a control group that was matched on age and verbal intelligence. In contrast, evidence suggests that in adults there is an opposite relation between the SNARC effect obtained in a parity judgment task and mathematical proficiency (Hoffmann, Mussolin, Martin & Schiltz, 2014) with smaller SNARC effects in math-proficient participants, and no mediating effect of visuospatial working memory capacity. The authors attribute this to the fact that those proficient in math are more efficient in inhibiting the magnitude information which is irrelevant in a parity judgment task (see also Hoffmann, Pigat, & Schiltz, 2014). Yet, the Bachot and the Hoffmann studies remain essentially correlational in nature and don't directly address the link between space and mental arithmetic. A recent study used fMRI to directly assess the involvement of the neural circuits of spatial processing in complex mental arithmetic (2-digit addition and subtraction). Knops, Thirion, Hubbard, Michel & Dehaene (2009) used multivariate decoding to distinguish the patterns of activation in parietal regions between leftward versus rightward eye movements. Interestingly these same patterns also distinguished between subtraction (associated with leftward) and addition (associated with rightward), suggesting the involvement of mechanisms of spatial attention in mental arithmetic. To what extent this reflects the movement of spatial attention over working memory positions or over long-term number representations needs to be determined. Recent theories of working memory even suggest that the distinction between working and long-term memory may not be that strict after all. Theories like the one of Cowan (1999) or Oberauer (2009) or suggest that working memory builds on activations in long-term memory with mechanisms of attention operating on these pre-activated segments of long-term memory (see also D'Esposito & Postle, 2015).

Clearly, a lot of work needs to be done to establish the details of how number, space and working memory interact and to test how it relates to mathematical proficiency. Whether or not the mechanism of orienting attention in a spatially-oriented working memory sequence will prove to contribute to mathematical skills, it is an illustrative case of how constructing and testing functionally explicit models will permit progress to be made in advancing our understanding of *how* it is that working memory and mathematical skill might be related. It is also worth considering to what extent ordinal working memory processing also contributes to other achievement domains such as language development (Majerus, Poncelet, Greffe, & Van der Linden, 2006), and eventually may provide explanatory ground for explaining comorbidities between developmental dyscalculia and dyslexia.

3. Executive functions

For efficient mathematical learning and performance, it is necessary to be endowed with good sensory processing systems (to estimate numerosity or to encode numerical symbols) and efficient systems to store, maintain and access information in memory (for instance, to keep track of intermediate results of calculations), but of equal importance are the executive functions that control the way these information processing and storage systems are orchestrated to be optimally configured for dealing with requirements dictated by task and context, for instance, for removing the results of intermediate calculations from working memory when they are not necessary anymore (Hitch, 1978).

Numerous studies have confirmed the contribution of executive functions to efficient arithmetical processing. Correlational studies have found mathematical and arithmetical skill to be associated with individual differences in executive function. An excellent example is the finding Bull, Johnston & Roy (1999) arithmetic performance is correlated with scores on the Wisconsin card sorting task suggesting the involvement of inhibitory process in mental arithmetic. Other studies have used dual-task paradigms to show that arithmetic performance deteriorates when participants simultaneously perform a task that consumes executive resources. This has been shown to be the case for multi-digit addition (Imbo, Vandierendonck & De Rammelaere, 2007) and multiplication (Imbo, Vandierendonck & Vergauwe, 2007), but, intriguingly, also for single-digit arithmetic (e.g. De Rammelaere, Stuyven, & Vandierendonck, 2001). The latter finding suggests that the impact of executive functions also comprises relatively basic levels of processing and is not restricted to complex capacities like storage of intermediate outcomes as involved in carrying or borrowing (Hitch, 1978).

Although the existence of a link between executive control and arithmetic performance is clear, the literature on executive functions typically considers it a very heterogeneous construct comprising several independent sub functions (e.g. updating, task shifting, monitoring, etc.; Miyake, Friedman, Emerson, Witzki, Howerter & Wager, 2000). In the dual-task studies in particular, the applied executive load typically is not further specified and does not permit one to pinpoint precisely which executive functions contribute to efficient mental arithmetic.

At the same time, the specification of mental arithmetic at the processing level also remains rather vague. Processes like retrieval- and strategy-based calculation are distinguished but many questions remain unanswered: How exactly are these processes executed? Which representations do they depend on? How do they elapse over time? Which neural resources do they recruit from? Finding an answer to such questions is extremely difficult, especially if one takes into account that executive involvement is very much dependent on the nature of the task and may vary with age and/or level of skill (Raghubar et al., 2010).

Although the previous sounds somewhat discouraging it should not be a reason to abandon hope. Indeed, adding computational modeling and neuroimaging to the arsenal of instruments to study executive control has been shown to permit a level of theorizing that allows a detailed explanatory account of an important cognitive control function. Specifically, by imposing computationally derived and biologically plausible constraints, the executive function of performance adaptation has now become largely understood at a neurocognitive mechanistic level. Recently, this knowledge has been applied to the context of mental arithmetic.

Performance adaptation is the capacity to self-regulate with the goal of optimizing behavior. This form of self-regulation is often referred to as cognitive control. Cognitive control can be seen as the operation of top-down functions that configure the components of a cognitive system in such a way that they are adapted to efficiently deal with the task requirements. Cognitive control requires the coupled operation of a monitoring system and an adaptive system, together forming a closed loop system. The monitoring system keeps track of how well the participant is doing and on the basis of that information the adaptation system imposes top-down control to optimise performance. The neural mechanism that underlies this control loop has been rather well described with the anterior cingulate cortex (ACC) and the dorsolateral prefrontal cortex (DLPFC) being key structures. The ACC continuously monitors task performance and if problems in performance (a difficult or erroneous response) are detected, then a signal is sent to the DLPFC which in turn will then impose top-down changes on the neural networks involved in task execution in order to optimize the efficiency of task performance with reduced risk of committing errors (Botvinick, Braver, Barch, Carter & Cohen, 2001). This mechanism has been mainly investigated with standard conflict tasks like the Stroop task, the Simon task or the flanker task, in which relevant stimulus aspects (e.g. ink color) need to be processed in the context of irrelevant stimulus aspects (e.g. color word) that may interfere with the processing of the relevant information. Recently, this framework has begun to be applied to the context of arithmetic performance.

Desmet, Imbo, De Brauwer, Brass, Fias & Notebaert (2012) investigated the behavioral consequences of errors in mental arithmetic, more precisely in verification of multiplication facts in which participants have to indicate whether a presented answer for a single-digit multiplication problem is correct or not (e.g. 4x5=20, or 6x7=48). It was observed that accuracy improved and reaction times slowed down on trials that followed errors. This was the case for errors that were committed by the participant, but also for trials in which an erroneous answer was proposed (e.g. 8x7 = 48), provided that the incorrect answer was table-related (i.e., a correct answer to another simple multiplication problem). This finding clearly supports the fact that cognitive control processes are at play when people solve even simple arithmetic problems.

A recent neuroimaging study confirms the involvement of ACC and DLPFC while solving arithmetic problems. Ansari, Grabner, Koschutnig, Reishofer & Ebner (2011) found stronger activation of ACC and bilateral DLPFC when participants committed an error while solving simple arithmetic problems of any operations. Interestingly, the right DLPFC was found to be modulated by mathematical competence as measured by a standardized mathematical test with highly competent individuals activating this area more on an incorrectly solved trial than less skilled individuals, suggesting efficiency of error detection is related to overall mathematical competence, or that individuals who are sensitive to errors develop stronger mathematical skills.

Rinne and Mazzocco (2014) established a developmental link between cognitive control and proficiency. In a longitudinal study they found that the successful detection of errors contributes to the development of arithmetic proficiency from grades 5 to 8. More specifically, they investigated the extent to which a good alignment or calibration between confidence in judgments of arithmetic performance and the accuracy of those judgments is related to the development of arithmetic skill. Calibration was shown to be related to performance, that it was particularly poor in children with mathematics learning disability and calibration in grade 5 predicted gains in arithmetic accuracy from grade 5 to grade 8.

It is clear that cognitive control and self-regulation contribute to mathematical skill. It is interesting to see how a neurocognitive framework has proven to be inspirational to start to form an initial picture of the underlying mechanisms. Yet, it is also important to realize that the models that are developed in the context of basic laboratory tasks don't necessarily transfer to the context of mathematical skill. Laboratory tasks are quite simple and often don't require much more than mapping a stimulus to a response, without much variety in solution strategies. In contrast, arithmetic and math often engage tasks that are more complex and can be solved by multiple procedural strategies (Lemaire & Siegler, 1995). An interesting avenue for further research could be to see how quality of performance determines strategy selection (Uittenhove & Lemaire, 2012; for a similar idea in a developmental perspective, see Qin, Cho, Chen, Rosenberg-Lee, Geary, & Menon, 2014).

4. Discussion and conclusions

Above I listed a number of neurocognitive components that are meaningfully related to mental arithmetic and mathematical processing and can reasonably be expected to be contributing factors of achievement and performance levels. Certainly, this list is not complete. There have been recent advances in understanding the memory mechanisms that are involved in the learning and retrieval of basic arithmetic facts. An important proposal has been made by De Visscher & Noël (2014a) who specify sensitivity to interference in memory as an important determinant of efficient storage and retrieval of multiplication facts. The nature of the number system results in a high degree of similarity among all arithmetic problems, and this in turn creates the potential for proactive interference that can hinder efficient storage of the arithmetic tables. Children who are particularly sensitive to such interference may experience difficulties memorizing or retrieving basic arithmetic facts (De Visscher & Noël, 2014b), a cardinal feature of mathematical learning disabilities (Geary, 1993). In line with this, there are studies that show that intrusion of related information is common when these children attempt to retrieval addition or multiplication facts (Barouillet, Fayol, & Lathulière, 1997; Geary, Hamson, & Hoard, 2000). Another domain where considerable progress is to be expected is the study of the contribution of general learning systems, like the hippocampus for memory formation or the basal ganglia for procedural learning. A recent study describes results that emphasize the fruitfulness of this path. Supekar, Swigart, Tenison, Jolles, Rosenberg-lee, Fuchs & Menon (2013) found that hippocampal volume and the way the hippocampus is functionally connected to prefrontal areas an to the basal ganglia is predictive of performance gain induced by a math tutoring program in grade 3 children.

The picture that arises from this functional analysis clearly has a broader scope than the idea of a unique explanatory factor determining mathematical competence, specifically the fidelity of number representations in the ANS. Essentially, it states that one can be endowed with a very sharp and efficient ANS, but efficient use of this system is dependent on many other, poorly understood brain and cognitive systems. Of course, my view that a broad spectrum of related neurocognitive components needs to be considered is not a plea to dismiss the importance of a well-functioning system for quantity representation. To the contrary, quantity representation is a vital component of number knowledge and how it can develop and be learned (see for instance, vanMarle et al., 2014, who suggest that the ANS supports children's initial learing of numerical symbols (e.g., number words) and their meaning (i.e., their cardinal value) but then becomes less important as children become more proficient with formal, symbolic mathematics). Yet, I believe that it should be seen as a component in the context of an ensemble of other components that together determines what level of mathematical proficiency can be achieved. It is the study of these interactions that opens up interesting perspectives. Indeed, the efficiency of some components is likely to have an impact on the limits of representational accuracy that can be achieved with practice or training. For instance, with poorly developed systems to map digits to quantity representations (Noël & Rousselle, 2011), it is well possible that the quantity representations don't receive the proper input needed to increase the acuity of these representations. Alternatively, it is not unthinkable that inaccurate quantity representations put heavy demands on other cognitive components, such as executive control.

Compared to a single-component view, a multi-component framework leads to a considerable increase in the degrees of freedom for theory development. Although this can be viewed as a significant disadvantage from a pragmatic point of view, a certain degree of theoretical complexity is the only way to fundamentally increase our understanding of the multifaceted nature of mathematical cognition. With increasing complexity and number of components it becomes progressively difficult to decide on the validity of one theory over the other. An important way out is to nail down the characteristics of the contributing components. This can be achieved by appealing to something other than the behavioral data that one wants to account for. In this respect a neural specification of the characteristics of the proposed components can provide the necessary constraints to limit the number of theoretical accounts (Anderson, 1978). Here, a lot of work has already been done, in the sense that the neural underpinnings of quantity representation have been described in rather good detail. For the other components we aren't quite as far yet, but I believe that, as I have tried to indicate above, some groundwork has been laid. By further refining our understanding of the neuro-functional organization of these other cognitive components, we can increasingly constrain the number of viable theoretical frameworks and ultimately come to a satisfactory understanding of how the synergistic interactions among several cognitive components permit the mastery of mathematical skills in all their facets, including how they develop – both normally and atypically as in dyscalculia or disability.

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Figure Captions

Figure 1: Three consecutive stages of processing visual numerosities are displayed. After visual input (consisting of a collection of dots), elements are first located in space (red). Next, a number-sensitive coding stage accumulates the information available in the location map (green). In a third stage, number-selective neurons identify the accumulated number of elements. Adapted from Roggeman et al. (2011).

Figure 2: Participants first have to encode a series of numbers into working memory. During the retention interval they perform a dot detection task. After the fixation cross, a number cue is flashed briefly. If the number belongs to the memorized set, participants have to detect the appearance of a dot, in which case they have to press a button. After the retention interval a number of questions are asked to evaluate if the participants had correctly memorized the series of numbers. Adapted from van Dijck et al. (2013).

Figure 1

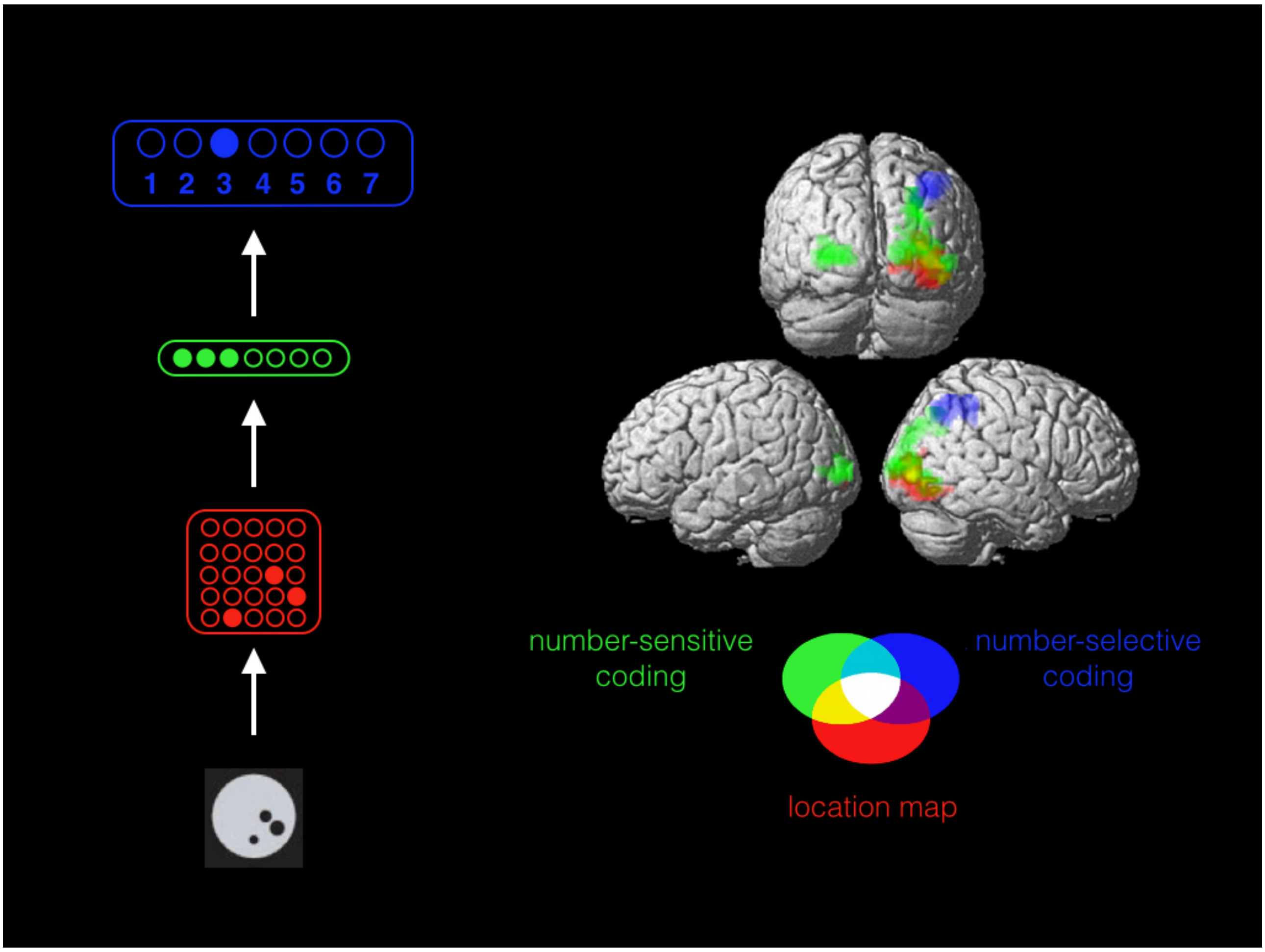
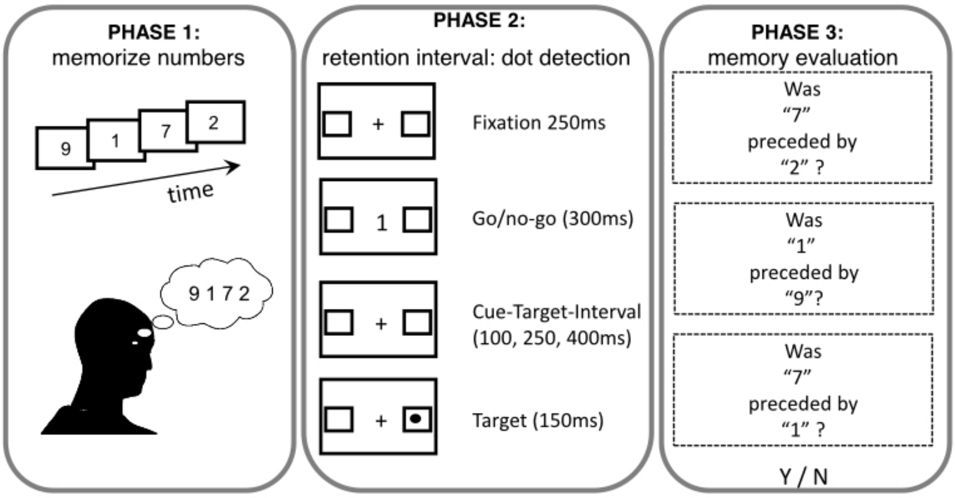

1 2 3 4 5 6 7
number-sensitive
coding
number-selective
coding
location map

Figure 2


PHASE 1:
memorize numbers
9
1
7
2
time
9 1 7 2
PHASE 2:
retention interval: dot detection
Fixation 250ms
1
Go/no-go (300ms)
Cue-Target-Interval
(100, 250, 400ms)
Target (150ms)
PHASE 3:
memory evaluation
Was
"7"
preceded by
"2" ?
Was
"1"
preceded by
"9"?
Was
"7"
preceded by
"1" ?
Y / N