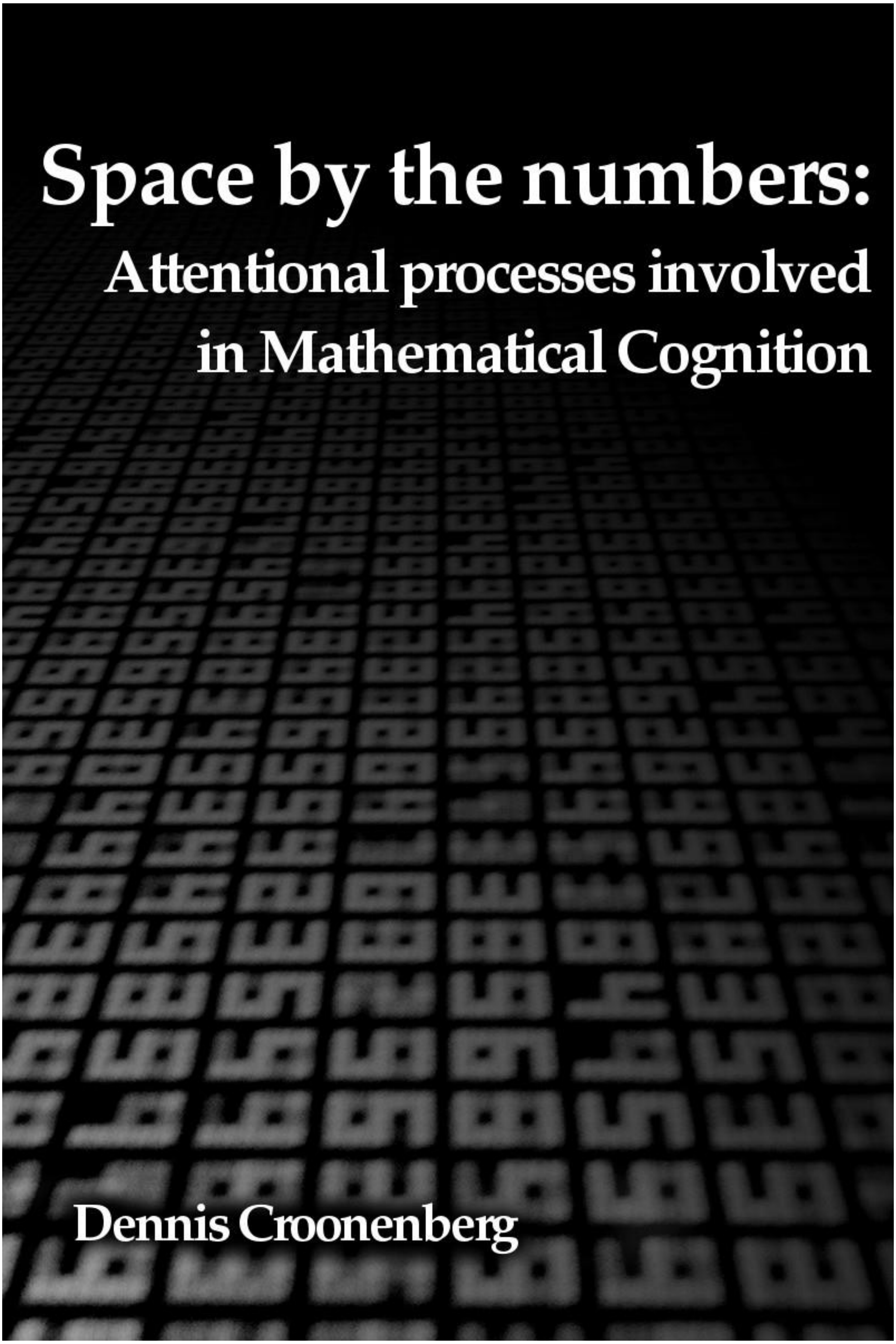

Space by the numbers: Attentional processes involved in Mathematical Cognition

Dennis Croonenberg

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Dennis Croonenberg

Born on 4 November 1983 in Heerlen (The Netherlands)

SPACE BY THE NUMBERS:

ATTENTIONAL PROCESSES INVOLVED IN MATHEMATICAL COGNITION

Space by the Numbers:

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Dennis Croonenberg

Supervisors

Prof. Dr. Alex Sack (University of Maastricht, The Netherlands)
Prof. Dr. Romain Martin (University of Luxembourg, Luxembourg)
Prof. Dr. Christine Schiltz (University of Luxembourg, Luxembourg)

Defense committee

Prof. Dr. Silke Göbel (University of York, United Kingdom)
Prof. Dr. Martin Fischer (Universität Potsdam, Germany)
Prof. Dr. Alex Sack (University of Maastricht, The Netherlands)
Prof. Dr. Romain Martin (University of Luxembourg, Luxembourg)
Prof. Dr. Christine Schiltz (University of Luxembourg, Luxembourg)

The author declares that all the work contained in this manuscript is his own and all sources are properly cited.

Dennis Croonenberg

Abstract

Numerical and spatial abilities have been correlated on many occasions. People who tend to be more proficient at spatial tasks also tend to be more proficient at mathematical operations and understanding of numbers. The current work takes several approaches to describe this relationship in further detail by investigating the role of attentional systems and executive control with regards to the processing of numbers and quantities. In a first attempt to do so we provide two studies whose goal it was to replicate the classical association between Arabic digits and response modality (SNARC-effect) and the association between Arabic digits and attentional shifts (Attentional SNARC-effect).

In two further studies, we investigated the role of the Attentional SNARC-effect with regards to visual processing and consciousness. In the first of these studies, we made use of a backwards-mask to obscure a single Arabic digit from conscious processing, resulting in the loss of its spatial association in a line-bisection task.

Secondly, we used a novel binocular rivalry paradigm to suppress two lateral stimuli from conscious perception and found that the duration of suppression was influenced by the numerical magnitude of a single presented Arabic digit. Specifically, we found that a stimulus on the left side of space would return faster when the Arabic digit was lower than five and that the right side of space would exhibit the same effect when the Arabic digit was higher than five.

A crucial manipulation in these last two experiments was an adaptation to the original paradigm for measuring the attentional SNARC-effect. By adding a control-question on the magnitude or parity at the end of each trial, we ensured that the spatial effects would occur during these experiments. Furthermore, this effectively turned the experiments into working-memory tasks.

Finally, we tested the influence of a visuo-spatial working-memory task and an addition-task on fronto-parietal network associated with mathematical operations in an event-related fMRI-experiment. This experiment included members of three populations with different levels of mathematical proficiency (Children with Developmental Dyscalculia, Typically developing children and Typical Adults). We found that brain-areas associated with executive control and basic visual processing were affected differently for children with developmental dyscalculia, hinting at a deficiency in visuo-spatial processing in this particular group.

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General Introduction

Spatial ability describes the capacity to understand and remember spatial relations among objects (West, 1997). Whether it is distances, sizes, causal physical connections or locations, the human experience requires a daily usage and manipulation of spatial factors. This type of ability can be distinguished from other types of intelligence such as verbal ability, reasoning and memory skills but can rarely, if at all, be isolated from these (McGee, 1979). A rather striking phenomenon is the tight connection of spatial processes to mathematical ability which can express itself in many ways, even outside the frame of spatial mathematics such as geometry.

In a relatively recent longitudinal study it was found that participants who show higher spatial abilities during adolescence tended to get more mathematically oriented careers such as science, technology, engineering more often than those who do not (Wai, Lubinski, & Benbow, 2009).

A potential explanation for this is provided by Heathcote (1994), who suggested that spatially based visual imagery might be the foundation of arithmetic skills after observing that addition of multi-digit addends is interfered by visual spatial distractors; therewith implying that visualising a problem or procedure is key to understanding fundamental mathematical concepts. Although verbal skills have been found to be of some importance in arithmetic difficulties (McLeod & Crump, 1978) there is a higher correlation between arithmetic and spatial ability (Solan, 1987). A further confirmation of the link between visuo-spatial abilities and mathematical abilities comes from children with 22q11 deletion syndrome (De Smedt, Swillen, Verschaffel, & Ghesquiere, 2009). 22q11DS describes a genetic disorder that besides some physical abnormalities and slight learning disability causes considerable impairment of mathematical skills. These children have relatively normal reading abilities, but show great difficulty in performing spatial tasks.

Visuo-spatial working-memory in mathematical operations

Spatial tasks such as Corsi-block tapping and mental rotation are also associated to performance in arithmetic or mathematics (Casey, Nuttall, & Pezaris, 1997, 2001; Kyttälä, Aunio, Lehto, Van Luit, & Hautamäki, 2003; Reuhkala, 2001) and even physical sciences (Humphreys, Lubinski, & Yao, 1993) and engineering courses (Sorby, 2009). Crucially performance on both Corsi-block tapping and mental rotation-tasks are thought to be representative of working memory (WM) capacity. Both tasks will be described in more in detail below.

According to the classical WM-model by Baddeley and Hitch (1974) working memory is divided in a phonological loop that deals with verbal material, visuo-spatial sketchpad for dealing with visuo-spatial material and executive control, all of which have been associated with mathematical operations or strategies. This model has more recently been supplemented with a fourth system (the episodic buffer), that is proposed to integrate long-term memory with the mentioned WM-systems and functions by representing information in an episodic manner (Baddeley, 2000).

$$\hat{H} = \sum_{n=1}^{N} \frac{\hat{p}_n^2}{2m_n} + V(x_1, x_2, \cdots x_N)$$
$$= -\frac{\hbar^2}{2} \sum_{n=1}^{N} \frac{1}{m_n} \frac{\partial^2}{\partial x_n^2} + V(x_1, x_2, \cdots x_N)$$

Figure GI.1. *Formula to express the position of a quantum particle n in* X_n

Making use of visualisation as a strategy for tackling mathematical problems would require working-memory (WM) capacity, where special requirements are necessary for the Visuo-Spatial Working-Memory (VSWM) and Central Executive (CE). Mathematics as a discipline contains many visuo-spatial characteristics in that it uses many different visual operators to signify different types of concepts. Diagrams, curves and charts are used to express relations between two or more variables in a visual manner. But even mathematical symbols, logical operators and numbers have characteristic visual components (Skemp, 1986). When considering the formula in figure I.1, all operators, variables, constants and numbers have a spatial location that is indicative of the relation they possess with regards to other components. Consequently the value of a single variable can be deduced if all others are known. In order to make any kind of sense of this formula, the spatial relation of each of the components needs to be understood. Both adults and children are sensitive to these relations. For example, adults were more prone to violations of precedence rules in solving algebraic equations when the distances among terms were manipulated (e.g., 2+3-4 vs. 2 + 3 – 4)(Fisher, Borchert, & Bassok, 2011; Landy & Goldstone, 2007). The existing literature provides a firm basis for concluding that spatial ability and math share cognitive processes beginning early in development (Cheng & Mix, 2014). But maybe more importantly, to get a grasp of the spatial relations of all the components in mathematics, they all need to be represented in working memory.

A person's capacity in visuo-spatial working memory (VSWM) has been related to better performance on counting tasks (Kyttälä et al., 2003) number-line estimation (Geary et al., 2007) and general math performance (Alloway & Passolunghi, 2011; Gathercole & Pickering, 2000; Lachance & Mazzocco, 2006; Mazzocco & Myers, 2003; Meyer, Salimpoor, Wu, Geary, & Menon, 2010; Raghubar, Barnes, & Hecht, 2010),

VSWM has been proposed to process and store short-term visual and spatial information and is thought to operate on visualisation (Baddeley, 1992; Baddeley & Hitch, 1974). Comoldi and Vecchi (2003) divide the different VSWM functions into passive and active functions. The passive functionality refers to short-term storage of spatial information. Active functions refer to processing functions which can be characterised as visuo-spatial central executive functions and concern active operation or representation of spatial procedures that might not be inherently spatial. In literature on visuo-spatial ability there are two tasks (or its derivatives) that appear most often; the Corsi block-tapping task and mental rotation. The Corsi block-tapping task is a sequential WM-task in which a sequence of locations has to be remembered and reproduced by the participant. Classically this is done by having an experimenter tap physical blocks in order, displayed in front of the participant, and having the participant reproduce the blocks were tapped in the same order as the experimenter. Children who have trouble performing arithmetic tasks tend to achieve lower performances in the Corsi-blocks, providing evidence for the importance of WM in the context of acquiring arithmetic skills (McLean & Hitch, 1999)

The mental-rotation task requires participants to make a judgement of whether a two-dimensional representation of a three-dimensional figure is displayed twice on a page.

Crucially one of the two representations is turned on one or more of three axes. This requires that the participant has to mentally rotate the original figure in order to determine whether the two displayed figures are the same. It has been found that children who portray a lower performance on arithmetic tasks also perform lower on mental rotation-tasks (Comoldi & Vecchi, 2003) and that training children on this task transfers positively onto the missing problem task (e.g. fill in the missing term 5 + __ = 7) (Cheng & Mix, 2014). It should be noted that the results by Cheng & Mix (2014) were not replicated in a study by Hawes, Moss, Caswell & Poliszczuk (2015)

Recent functional Magnetic Resonance Imaging (fMRI) studies have elaborated these types of findings with several crucial insights. In children with developmental dyscalculia (DD), it was found that the intraparietal sulcus, middle occipital gyrus and inferior frontal gyrus portrayed lowered activation than age-matched controls when using an adaptation of the Corsi block-tapping task. Crucially, these areas were previously associated with the development of mathematical skills (Rotzer et al., 2009). Diminished neural activity of these specific areas could also be observed directly when children with DD perform numerical tasks (Kucian et al., 2006). A longitudinal fMRI study by (Dumontheil & Klingberg, 2012) provides further evidence for the causal role that intra-parietal sulcus neurons play in both VSWM and numerical operations. The authors reported that brain activity in the intra-parietal sulcus during a VSWM-task in six-to-sixteen year-old participants was predictive of participants' mathematical performance two years after scanning, even more so than their performance in behavioural tests.

In the current manuscript, an attempt is made to describe and expand upon the many complex ways that spatial operations, numerical processing and arithmetic interact. Specifically, it will describe how the processing of visual information is affected by or can affect the processing of Arabic digits or simple arithmetic.

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Part I:
Number-space associations

"We're all apprentices in a craft where no one ever becomes a master"

- Ernest Hemingway, The Wild Years

Introduction

The connection between the mathematical and the spatial is not restricted to general performance in certain fields of mathematics or specific mathematical tasks. An important field of study concerns a more inherent linking between numbers and space. We tend to learn mathematical operations as a string of procedures. Before a second operation can be carried out, the first one must have finished. But before this can take place, when developing early counting skills, we have to develop a sense of the sequential order in which the Arabic digits represent magnitude. According to the developmental model by von Aster and Shalev (2007) mathematical development begins with a basic grasp of number sense (cardinality).It continues to say that this is followed by the acquisition of linguistic and symbolic number representations by acquiring knowledge over number-words and Arabic digits during formal education. Finally it is argued that children acquire mental visuo-spatial numerical tools in order to cope with arithmetic problems. To test the development of numerical understanding in young infants many studies make use of a dishabituation paradigm, which has shown that infants as young as 5 months old are able to differentiate between small numerosities (two to six) (Starkey & Cooper, 1980) and subsequent research has shown that this ability is also present when infants are just one week old (Antell & Keating, 1983). Furthermore, it seems to be that neural mechanisms for discriminating between numerosities are already present at 3-months as change in numerosity induces a different pattern of evoked potentials in the right parietal lobe (Izard, Dehaene-Lambertz & Dehaene, 2008).

Another way of studying the development of numerical representation in development is by looking at distance effects. A distance effect describes the finding that when comparing two numbers for their size, the larger the distance in magnitude is between these numbers, the faster people tend to respond (Moyer & Landauer, 1967). Crucially, as mathematical development progresses, children between 5 and 10 years old become more accurate in discriminating between two sets of non-symbolic or symbolic quantities (Piazza, 2010; Holloway & Ansari, 2009; Landerl & Kölle, 2009; Ansari & Dhital (2006). Both symbolic and non-symbolic distance effects are correlated to performance in arithmetic, indicating higher arithmetic performance as discrimination improves, resulting in a lower weber-fraction (Holloway & Ansari, 2009; Halberda et al., 2008). Furthermore, it was shown that for symbolic distance effects this correlation is independent of age, intellectual ability, and speed of number identification (de Smedt, Verschaffel & Ghesquière, 2009).

When learning to make these representations of numerosity, we also learn to associate them with certain spatial aspects. Whether it is finger-counting, clock-reading or writing numbers horizontally or learning numbers in class via a number-line there are many examples which give numbers an inherently spatial characteristic. Of these, the horizontal ordering of numbers on a number-line is particularly interesting and the subject of a great amount of research. For instance, it was found that children's visuo-spatial skills are predictive of how well they are able to gather knowledge about a number-line during 1st and second grade. Furthermore, it was found that their spatial abilities at age 5 predict their performance in approximate calculation at age 8 (Gunderson, Ramirez, Beilock & Levine, 2012).

Spatio-Numerical Association of Response Codes (SNARC)

Sir Francis Galton (1881) described that some people make a personalized representation of numbers, which he called a number-form. However, these number-forms are relatively rare and occur in only 15% of the population (Seron, 1992) . There is however a stronger spatial correlate that has been established later. An entire body of evidence indeed suggests that people represent discrete numerosities as a mental number-line (MNL) (Dehaene, Bossini, & Giraux, 1993; which unlike the number-form people are not aware of (Hubbard, Piazza, Pinel, & Dehaene, 2005) but has been argued to aid the learning of numerical concepts (Booth & Siegler, 2008) and arithmetic (Gunderson et al., 2012; Verdine, Golinkoff, Hirsh-Pasek, & Newcombe, 2014). .

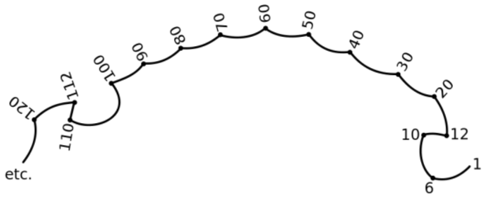

Figure I.2. *A number-form as described by Galton (1881)*

A striking piece of evidence for the existence of a MNL comes from the fact that people are faster in identifying the magnitude or parity of a single digit with their left hand if the number is small and faster with their right hand if the number is large. This particular piece of evidence is referred to as the Spatio-Numerical Association of Response Codes (SNARC) effect and it suggests that people tend to represent quantities on a linear number line with their own bodies at the midpoint (Berch, Foley, Hill, & Ryan, 1999; De Hevia & Spelke, 2009; Maria D de Hevia & Spelke, 2010; Dehaene et al., 1993; Fias, 2001; Fischer, 2003; Imbo, De Brauwer, Fias, & Gevers, 2012; Lourenco & Longo, 2009; van Galen & Reitsma, 2008). In this view, the SNARC-effect arises from a congruency between the mental-number line and laterality of the response modality (Keus, Jenks, & Schwarz, 2005). This would be similar to the Simon-effect, which describes the effect that people tend to be faster when the side of a laterally presented stimulus matches the hand that people have to use to respond (Gevers, Lammertyn, Notebaert, Verguts, & Fias, 2006; Simon & Rudell, 1967). One of the most striking findings to come from research linking numbers and space is the distorted representations of numerical space that occur in neglect patients following right parietal damage. Patients with hemi-spatial neglect due to right hemispheric lesions tend to visually neglect the left side of space (Unsworth, 2007). Zorzi, Priftis, and Umiltà (2002) found that, when participants were asked to estimate the middle between two numbers, neglect patients selected numbers to the right of the true centre, indicating that neglect not only affects the processing of physical space but also influences mental spatial operations. For example, when estimating the middle between 11 and 19, neglect patients suggest a midpoint of 17 or 18. Further evidence for a number-space interaction comes from experiments using line bisection tasks. In these tasks, healthy subjects had to indicate the middle of a line, while it was flanked by Arabic digits or non-symbolic arrays of dots. Although the flanking numbers or quantities are irrelevant to the task, adults show a spatial bias towards the larger number, irrespective of its lateral position (de Hevia, Vallar, & Girelli, 2006; De Hevia & Spelke, 2009; Fischer, 2001; Gebuis & Gevers, 2011).

Extending SNARC beyond a mental number line

There are some alternative explanations for the SNARC-effect that do not depend on the assumption of a MNL. Gevers, Verguts, Reynvoet, Caessens, and Fias (2006) proposed a computational model to account for the SNARC effect. This model consisted of three layers where the bottom layer represents numerical information and the upper layer represents response alternatives. The middle layer is responsible for conceptually categorizing numbers as small/large, odd/even, or any given category that is required by the task. These categorical representations are then associated with their corresponding alternative on a specific response dimension. Consequently, a number that is categorized as small or large will first activate an abstract spatial code such as “left” or “right” before activating a response. Similarly, Proctor & Cho (2006) argue that the SNARC effect is a result of intermediate categorisation of numerical cues as high and low or odd and even. As long as stimuli can be coded on a polar level (either positive or negative) a similar location-coding will occur. Both these explanations are in line with a response-discrimination account of spatial associations (Lammertyn, Gevers, Notebaert, Verguts & Fias, 2003; Santens & Gevers, 2008; Göbel, Johansen-Berg, Behrens, 2004) and speak against an account of the SNARC-effect that explains the spatial associations due to a direct mapping of a mental number-line onto visual space.

Another explanation that tries to account for spatio-numerical associations and SNARC-like effects places an emphasis on working-memory and ordinal sequences. This is based on experimental research that has shown that the spatial bias of numerical magnitude is dependent on the context of the task (Van Dijck, Gevers and Fias, 2009; Herrera, Macizo, & Semenza, 2008). For instance, it has been shown that the SNARC-effect reverses when participants are asked to imagine numbers on a clock-face, eliciting a stronger association of high numbers to the left side of space and low numbers on the right (Bächtold, Baumüller, & Brugger, 1998). Furthermore, the association of left or right for specific single digits depends on the range of numbers used (Dehaene et al., 1993; Fias, 1996) and the numerical reference they have to be classified against (e.g. higher or lower than for instance 4)(Nathan, Shaki, Salti, & Algom, 2009).

This flexibility in spatial associations due to task-instruction has led van Dijck and Fias (2011) to the proposition that working-memory resources that are being recruited during the performance of a spatial task are the foundation for SNARC-like effects. They found evidence that responding to a stimulus from a sequence of stimuli which had to be held in WM was influenced by its position in that sequence. More specifically, participants reacted faster and more accurately with their left hand to the first stimulus in a sequence and faster and more accurately with their right hand when the stimulus was last in that sequence.

When the sequence consisted of Arabic digits this effect occurred independent of the magnitude. Furthermore, this effect also occurred when there was no numerical information in the presented sequence and the stimuli solely consisted of written words (van Dijck & Fias, 2011).

Further evidence for spatio-numerical associations was also found with other response modalities than the simple left/right button presses used in the classical SNARC setting. For instance, SNARC-related effects have been found for pointing (Fischer, 2003; Ishihara et al., 2006), eye-movement (Fischer, Warlop, Hill, & Fias, 2004), line bisection (Calabria & Rossetti, 2005) and grasping (Andres, Davare, Pesenti, Olivier, & Seron, 2004) providing evidence for an influence of numerical magnitude over motor-planning.

Several pieces of evidence hint towards an (at least partially) spontaneous and pre-determined origin of spatio-numerical associations. A first indication lies in the fact that they seem to be present very early in life (Lammertyn, Reynvoet, Dupont & Orban, 2003). Furthermore, there seems to be an anatomical overlap in cortical regions involved with numerical processing and spatial tasks (Dehaene, Piazza, Pinel & Cohen., 2003; Fias, Lammertyn, Reynvoet, Dupont & Orban, 2003). A third peculiarity that our brains might pick up is that due to the predominant use of a base-ten counting systems (and more complex mathematical reasons that fall outside of the scope of this work) multi-digit numbers tend to predominantly start with a small digit and end with higher digits, suggesting a natural systematic association of symbolic quantities and space (known as Benford's Law, see: Beepe, 2015; Shaki & Fischer, 2008, Fischer, Mills & Shaki, 2010).

There are however many sources that describe different more experience-based accounts for the nature and spatial orientation of spatio-numerical associations. A well-known influence is reading direction. It has been shown on several occasions that the association between a certain side of space and numerical magnitude (as can been seen in the SNARC-effect) depends on reading direction. For instance, in Arabic cultures (that read right-to-left) lower numbers are associated with the right side of space and higher numbers with the left (Zebian, 2005). Quite strikingly, in bilingual Russian-Hebrew readers it has been shown that participants who displayed an initial left-to-right SNARC-effect that occurs after reading Cyrillic is greatly diminished after reading Hebrew (right-to-left), indicating that the association is influenced by reading-direction in a flexible manner (Shaki & Fischer, 2008).

A second experience-based account of spatio-numerical origins concerns the use of finger-counting. For instance, it has been found that the habit of starting to count on either left or right hand can influence the strength of an individual SNARC-effect (Fischer, 2008) and lead to faster reaction times when numbers have to be typed in congruently with a participant's finger-counting strategy, rather than in line with a standard number-line (Di Luca, Granà, Semenza, Seron & Pesenti, 2007). It has even been argued that finger-counting might be the sole proprietor on spatio-numerical associations as reading-direction might not be consistent between words and multi-digit numbers (as is done in Hebrew), spatio-numerical association exist before formal reading training has begun and can be diminished with simple experimental manipulations (Fischer & Brugger, 2011).

Finally, it must be noted that spatial processing of quantities is not only present in humans as it seems to be the case that other animals make spatio-numerical associations as well, suggesting a biological origin of spatio-numerical associations. An example of this is the tendency of 3-day-old chicks to start on the left side when presented with 5 identical trays of food (Rugani, Vallortiga, Vallin & Regolin, 2011) and associate large numbers with the right side of space (Rugani et al., 2014, 2015). Chimpanzees and rhesus monkeys also seem to associate the left side of space with small numbers (Adachi, 2014, Drucker & Brannon, 2014).

The first empirical study described in this work probes the context-dependence of SNARC effects with respect to the effector by making a direct comparison between a classical SNARC-effect obtained with left/right button presses and the influence of numerical magnitude on more complex motor-planning. It does so by having participants use their left and right hand to make a motion towards the left or right to judge the parity of a centrally presented digit. This way, it could be tested whether the lateral bias of the classical SNARC-effect was modulated by the task-instruction. We hypothesized that when participants were instructed to move a single effector to the left or right instead of using both the left and right hand to make a response, they would no longer portray a faster reaction with their left hand to low numbers and be faster with their right hand to high numbers. Instead, they would portray faster leftwards motion when numbers were low and faster rightward motion when the presented digit was high. Furthermore, by implementing an instruction that required a reaction with left and right index finger (e.g. classical SNARC) we could show that a SNARC-effect can be induced in the same population.

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I.1

Introductory report of pilot data:

The Joy of SNARC-hunting: A directional motor-planning account of the SNARC-Effect

Dennis Croonenberg[1,2], Romain Martin[1], Christine Schiltz[1]

1. Université du Luxembourg, Faculty of Language and Literature, Humanities, Arts and Education, ECCS, Esch-Sur-Alzette, Luxembourg
2. Maastricht University, Department of Cognitive Neuroscience, Vision and Awareness Lab, Maastricht, The Netherlands

Abstract

When asked to judge the parity or magnitude of an Arabic digit people tend to respond faster with their left hand when the digit is small (<5) and faster with their right hand when the digit is large (>5). This is known as the SNARC-effect (Spatio-numerical association of response codes) and has been shown to exert an influence over directional motor-planning. The current experiment extends these results by implementing the use of a joystick, operated by either the left or right hand, in addition to a classical button-based test. We were able to replicate a classical SNARC effect eliciting a faster right-handed response to the numerals 8 and 9 and faster left-handed response to 1 and 2. Furthermore, we were able to find a SNARC-effect for direction of movement -but only for the right hand. This indicates that the influence of magnitude-processing on directional motion is dependent on the context of the task.

Introduction

The mental number-line (MNL) hypothesis postulates that humans make a mental spatial representation of numbers ordered from left to right in western cultures (Dehaene, Dupoux, & Mehler, 1990; Restle, 1970). The spatio-numerical association of response codes (SNARC) effect is argued to be a reflection of the existence of a MNL and describes the phenomenon that when participants are presented with a single Arabic digit which they have to categorise as being high or low (or alternatively odd or even) they tend to respond faster with their right hand to high numbers (higher than 5) and faster with their left hand to low numbers (lower than 5) (Dehaene, Bossini, & Giraux, 1993). This effect is proposed to be due to compatibility between the effector (left or right hand) and the spatial representation of the digit on the MNL, similar to a Simon-effect (response time facilitation through congruence between target and response button location (Simon & Rudell, 1967)). Several electro-encephalography (EEG) studies linked this lateralized SNARC-effect to early response-selection stages of processing (p300) and the lateralized readiness potential (Gevers, Ratinckx, De Baene, & Fias, 2006; Keus, Jenks, & Schwarz, 2005). These findings suggest that spatio-numerical associations arise from interference with and/or facilitation of motor-planning and response selection. Further evidence for the influence of spatio-numerical associations on motor planning derives from many experiments employing motor-related tasks including eye-movement (Fischer, Warlop, Hill, & Fias, 2004), manual line bisection (Calabria & Rossetti, 2005) and grasping (Andres, Davare, Pesenti, Olivier, & Seron, 2004).

These motor-related effects could be interpreted as a result of embodied cognition, which hypothesizes that knowledge can be encoded as a set of motor-actions or sensory representations (Foglia & Wilson, 2013; Wilson & Foglia, 2011). For numerical knowledge, the influence of numerical magnitude as seen by the SNARC-effect seems to be such a type of encoding (Fischer, 2012; Fischer & Brugger, 2011). Further evidence for this was provided in a pointing task by Fischer (2003), where participants had to respond to a centrally presented numerical cue by moving the index finger of either the left or right from a central starting-point to lateralized targets. (Fischer, 2003; Ishihara et al., 2006). This type of pointing-task provides a practical instrument to dissociate between motor-planning of a movement and its on-line visuo-motor demands by separating between the onset of a movement and its execution. However, both Fischer (2003) and Ishihara et al. (2006) do not differentiate between preferred and non-preferred effector.

In the current experiment we offered a classical parity judgement task through the use of a joystick, manipulated with the left and right hand separately. This was done to offer a comparison between a classical SNARC-effect and a spatio-numerical association between numerical magnitude and lateral motion. In other words, we investigated whether the effect of a faster response with the left hand to low digits and a faster response with the right hand to high digits would still be present when the instruction was to respond by moving a single hand to the left or right (i.e. choose between two opposite movement directions, instead of choosing between two effector sides). We hypothesized that when participants were instructed to move a single hand bi-directionally; there would no longer be an association of left hand with lower numbers and right hand with higher numbers. Instead an influence of numerical magnitude would express itself on directionality of the movement such that participants are faster leftwards for responses when classifying low numbers and faster for rightwards response when classifying high numbers independently of the response hand's side. We compared the derived results to a classical lateralized SNARC task using either left or right hand to press a button on the left or right side of space. We argued that when these hypotheses rang true it would be evidence that a spatial influence of numerical magnitude on motor-actions is not limited to choice of effector but instead affects spatial motor-planning.

Methods

A total of 27 right-handed participants (20 female, 7 male) volunteered for this experiment. All participants were aged between 18 and 25 and provided written informed consent before experimentation took place. Participants where fully debriefed on the purpose of the experiment after participation. The local ethical committee (ECP) of the University of Maastricht approved the study. Participants were instructed to reply to the task using a generic US-international keyboard for the lateralized button conditions and a joystick for the directional conditions.

In both of the conditions participants were shown one of four numbers (1, 2, 8, or 9) which they had to categorize as either "even" or "odd. Categorization of a number occurred by either pressing the left 'Z'-button or right '/'-button or by moving the joystick to the left or right side using either their left or right hand in consecutive conditions. Whether odd or even was associated with a left or right response was counterbalanced between participants. The same was done for the order of the two tasks (i.e. the classical left/right button press or directional movement using a joystick). Each number was repeated 40 times per condition, cumulating to a total of 640 trials over both of the conditions.

In each trial, the digit was presented for 300 ms. participants were instructed to respond as fast and accurately as possible after the onset of the digit. To combat rhythmicity in the task, inter-trial intervals which only contained a fixation cross in the middle of the screen were presented after responses, differing randomly between 1 and 4 seconds. The reaction time for each participant was measured according to how long it took to press a button or move the joystick past a 45^{o} angle to the left or right.

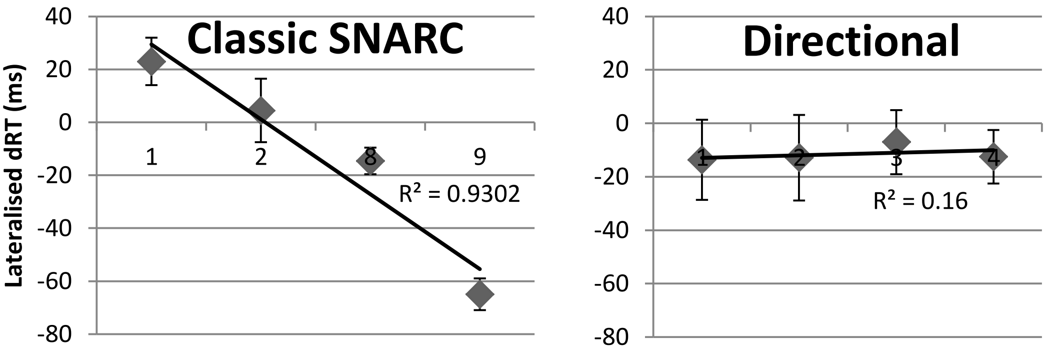

Figure I.1.1. Lateralized dRTs (right hand – left hand) for theclassical SNARC and directional task. Participants show a SNARC-effect in the classical task by showing a negative slope, indicating faster right-handed responses to high numbers and faster left-handed responses to low numbers.

Results

For both of the conditions, differential reaction times (dRTs) were calculated to express a preference for direction or response side. For the lateralized (button-press) response-task this was done by averaging RTs separately for each digit and subtracting the left-handed reaction time from the right-handed reaction time. For the directional (joystick movement) task this was done by subtracting the time to make the leftwards motion from the rightwards motion for each individual hand as well as subtracting average motion time for the left hand from the right.

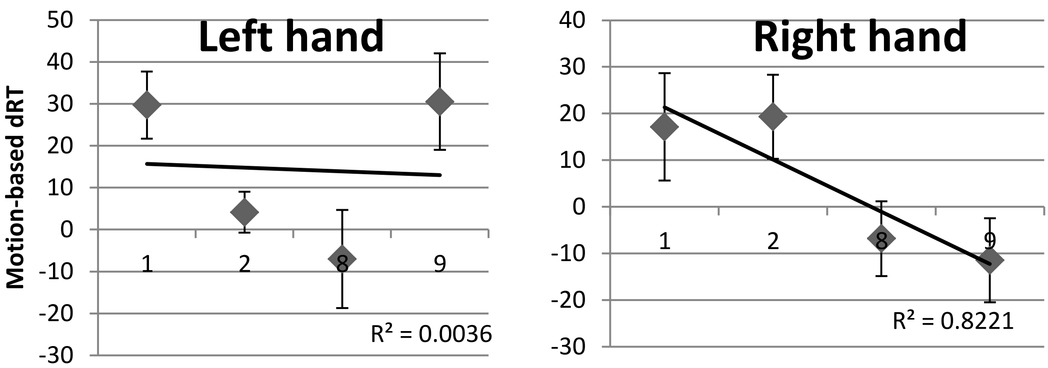

Figure I.1.2. Directional DRTs (rightwards motion – leftwards motion) for the directional task. Participants show a SNARC-effect the right hand, but not for the left.

The classical SNARC-task yielded a significant linear fit (R^2 = 0.976) whichshowed that the response time was predicted by the numerical magnitude of the digit cue, showing a significantly negative slope (F(1,2) = 89.3, p=.01) therewith confirming a replication of the SNARC-effect in this task. For the directional task, participants did not portray a classic SNARC-effect. However, we did find a linear fit for directional motion for the right hand (R^2 = 0.93) and not for the left (R^2= 0.217), indicating that numerical magnitude facilitates congruent motion when the right pre-dominant hand is used. Repeated measures ANOVA revealed a significant interaction between the condition and response side/motion (F(1,26)=2.56; p=0.02). To further express the strength of spatio-numerical associations RTs in each task were coded for congruence. This was done by taking the dRTs for each participant and negating the outcomes for the higher numbers and calculating an overall average. This way a negative dRT (e.g. a bias in RT congruent with numerical magnitude) for higher numbers would become positive. Subsequently dRTs for each number were averaged and tested against zero in a one-sided T-test. Results show a significant difference from zero in the right hand for the joystick-task (t(26) = 2.31 , p=0.05) and the classical SNARC-task (t(26) = 3.50 , p=0.03) but not for the left-hand (t(26) = -0.29 , p=0.83) and the subtraction or right handed RTs minus left handed RTs for the directional task (t(26) = 0.98 , p=0.61).

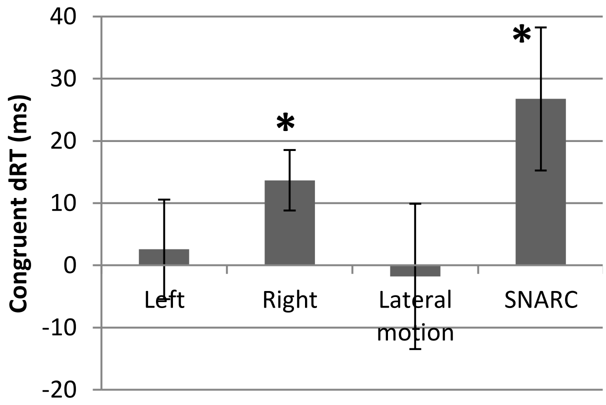

Figure I.1.3. Test of congruency for left hand, right hand and right had minus left hand (lateral motion) for the directional task versus the classical SNARC task

Discussion

The current experiment confirmed the influence of numerical processing on motor-planning as described by Fischer (2003). Furthermore we were able to show that in right-handed participants this effect was specific to the right-hand. In contrast to Fischer (2003), who only found a number-congruency effect for high numbers, we were able to induce a spatial bias for both high and low numbers in the present set-up. We therefore propose that the effect of numerical magnitude on motor-planning for manual tasks could be largely centred around the preferred hand when the task is performed unilaterally. Wiemers, Bekkering & Lindemann (2014) already made important inferences about the association of unilateral directional motor-responses with numerical processes. In their study, participants had to answer on addition or subtraction problems while either moving their right arm or eyes horizontally or vertically. They found that when vertical motion was congruent with the arithmetical performance (i.e. moving the arm up for addition, or downwards for subtraction) efficiency scores increased compared to incongruent motion. The authors suggest that although both horizontal and vertical associations are activated when performing arithmetic, the vertical association for addition and subtraction is stronger (Wiemers, Bekkering & Lindemann, 2014). The current experiment does not make use of vertical motion and it is therefore not possible to make inferences about such motion.

Classically, the SNARC-effect is described as an influence on lateralized responses concerning a left-handed or right-handed response. Crucially, this effect describes a difference in reaction time for either the left or right hand that is influenced by the magnitude of a single digit. In the current experiment we show that this association is diminished when participants need to make a lateral motion using a single hand. In this case there is no longer a bias for the left or right hand, but only for leftwards or rightwards motion. We further feel that the task we used offers an alternative to pointing tasks, as it provides a slightly less demanding task for participants. In contrast to keeping one hand at a steady position on a screen, removing it and placing it at another position, the use of a joystick only requires a quick flick of the wrist.

In a hierarchical explanation Fischer (2012) differentiates between three concepts regarding the embodiment of numerical information; ‘groundedness’, ‘embodiedness’ and ‘situatedness’. In this explanation, the ‘groundedness’ of knowledge refers to that which is universal and restricted in human cognition, taking as an example that it would take longer to rotate an object over a greater angle or that a greater quantity of something would take up more space. The SNARC-effect is mentioned as an example of ‘embodiedness’ of numerical information as it represents an influence of numerical magnitude on certain motor-tasks (Fischer & Brugger, 2011). ‘Situatedness’ describes a series of top-down and bottom-up processes that influence knowledge-activation dependent on the situation or position that the body is in (for instance laying down vs. sitting upright).

In the current experiment it seems to be the case that there is some amount of interaction between the situatedness and embodiedness while leaving the groundedness of numerical information intact. Although, the embodiment of the numerical magnitude is still reflected in reaction times regarding the left and right side of external space, the way in which it expresses itself seems to be dependent on the context of the experimental setup. In the current experiment the classical SNARC-effect disappears when the situation of the experiment requires participants to answer using a single hand. In conclusion, the current results give an interesting account on the flexibility of spatio-numerical associations and show that the context of the task has a great influence on whether or not a facilitation of lateral effectors will occur due to the processing of numerical magnitude.

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Part II:

The role of spatial attention in numerical processing and number-space associations

"If moderation is a fault, then indifference is a crime."

- Jack Kerouac

Introduction

Performance in arithmetic relies heavily on cooperation between attention and working-memory (Engle, Tuholski, Laughlin, & Conway, 1999; Garavan, 1998). For example, when the task is to add three-digit numbers mentally, it is crucial to focus on the ones in the first step, while holding the other digits in memory at the same time. Moreover, when considering that numerical information might be oriented on a mental number-line, visuo-spatial attention comes into play. Fischer, Castel, Dodd, and Pratt (2003) found that the simple presentation of small numbers (centred on a screen) speeded subsequent detection of peripheral stimuli in the left visual field, while the central presentation of larger numbers speeded detection in the right visual field, suggesting that number processing causes shifts in covert spatial attention. These shifts of attention had been shown before when using arrows or eye-gaze as directional cues in similar tasks that require detection or classification of lateral stimuli (Galfano et al., 2012; Posner, 1980; Ristic & Kingstone, 2012).More recently, their existence in association with passively viewed number cues has been confirmed in several independent studies (e.g. Galfano, Rusconi, & Umilta, 2006; Ristic, Wright, & Kingstone, 2006; Dodd, van der Stigchel, Adil Leghari, Fung, & Kingstone, 2008; Dodd, 2011; van Dijck et al., 2014; Hoffmann et al., 2015; but see also Zanolie & Pecher, 2014 for a failure to replicate the original study and the related comment by Fischer & Knops, 2014). Moreover it has been suggested that digits belong to the same family of stimuli inducing automated symbolic orienting as other central symbolic cues such as arrows or gaze (even though probably at another end of the same spectrum, as proposed by Ristic et al., 2006).

Further evidence for anatomical overlap between numerical and spatial processes can be found in studies involving patients with spatial neglect as well as studies on pseudo-neglect in healthy participants. While neglect patients ignore features on the left side of real (Nichelli, Rinaldi, & Cubelli, 1989) and representational (Bartolomeo, Bachoud-Lévi, Azouvi, & Chokron, 2005) space, the general population also shows an attentional bias, but in the opposite direction. This tendency to overestimate the left side of space, known as pseudo-neglect (Bowers & Heilman, 1980), appears to share a similar cognitive (McCourt & Jewell, 1999) and neural (Foxe, McCourt, & Javitt, 2003) basis with clinical neglect. Like neglect, pseudo-neglect distorts the MNL. Using a forced-choice number bisection task, Loftus, Nicholls, Mattingley, Chapman, and Bradshaw (2009) demonstrated that participants systematically overestimate the length on the left side of the MNL (Longo & Lourenco, 2007). The leftward bias for physical and MNL bisection is correlated within individuals (Longo & Lourenco, 2007) and, like pseudo-neglect for physical lines (Foxe et al., 2003) the neural basis of pseudo-neglect for MNL bisection lies in the right posterior parietal cortex (Göbel, Calabria, Farne, & Rossetti, 2006; Foxe et al., 2003).

An important finding with regards to the neural mechanisms concerning the relationship between attention and arithmetic comes from a study by Knops, Thirion, Hubbard, Michel & Dehaene (2009). They found that when a classifier was trained on saccadic eye-movement during an fMRI experiment, its performance was able to generalize to addition and subtraction. More specifically, classification of leftwards eye-movement generalized to subtraction and rightwards eye-movement to addition where performance was the highest in the intra-parietal sulcus. The authors concluded that arithmetic involves an operation along the mental number line resulting in preparatory activation of eye-movements. The idea that arithmetical processes are associated with shifts of visuo-spatial attention is also supported by the recent behavioural findings on mental arithmetic (Masson & Pesenti, 2014; Mathieu, Gourjon, Couderc, Thevenot & Prado (2015).

`The role of consciousness in researching number-space associations

Many studies on the nature of consciousness involve the use of unconsciously perceived stimuli. A widely used technique for dissociating awareness and stimulation is visual backward masking: A brief target-stimulus followed shortly thereafter by a mask. With appropriate timing and spatial arrangement of target and mask, the technique works very effectively on a wide range of stimuli such that an ordinarily visible target can be erased from visual awareness by the mask. It is commonly accepted that the mask 'halts' processing of the target, thereby abbreviating the target's effective duration. In contrast, when a mask precedes a target in time (forward masking) target invisibility is likely to result from reduction in effective target contrast at early stages of processing, not from disruption of central processing (Blake, 1989; Breitmeyer, Hoar, Randall, & Conte, 1984). Another important way of manipulating conscious perception is that of rapid serial visual presentation (RSVP). Following a similar logic as masking-experiments, RSVP depends on close temporal proximity of multiple visual stimuli in order for one stimulus to be perceived unconsciously, known as an attentional blink (Broadbent & Broadbent, 1987). A third way to manipulate whether stimuli are being processed consciously is by using binocular rivalry. When presenting different (contrasting) stimuli to the left and right eye respectively, people do not perceive a blend of those two images consciously, but only a single one of the stimuli. Both the stimuli will remain in consciousness for discrete amounts of time and alternate (Tong, Meng, & Blake, 2006).

Apart from the extensive exploration of spatial neglect, which mostly focuses on spatial biases with regards to numerical processing not the numbers themselves, systematic studies on the nature of conscious versus unconscious processing of numerical magnitude are rare. Although there have been studies that mask Arabic digits, most of these are not concerned with the nature of numerical processing itself. There are, however, a few exceptions: Dehaene and Naccache (2001) found that activation in the parietal lobe codes for numerical quantities of both unconsciously and consciously perceived numbers using both sub- and supraliminal primes. Furthermore, by utilizing both a forward and backward mask to unconsciously prime people with numeral finger configurations, Di Luca and Pesenti (2008) found that people were faster to judge the magnitude of an Arabic numeral when the numerical magnitude was congruent with that of the prime than in the incongruent condition. Both these studies show that numerical information can still be processed to a certain degree, even when they are perceived unconsciously.

The following three chapters describe the modulation of spatial attention that is associated with numerical magnitude processing. The latter two of these chapters are placed within the context of conscious versus unconscious visual processing.

In order to elaborate on an attentional SNARC-effect we first set out to replicate the initial study by Fischer et al. (2003) in chapter II.1. Unfortunately, we were unable to do so despite several attempts and rigorous matching of experimental conditions. Even though this chapter describes a null-result, it formed the basis for formulating the approach taken in the next two chapters.

In chapter II.2 'Masked magnitude: the influence of masked Arabic digits on line bisection', we implemented backwards masking to see if the absence or presence of visual awareness influenced the spatial bias that would occur. This was done in order to study whether the spatial bias that occurred due to the numerical magnitude of a briefly presented number-cue would be affected by a diminished amount of processing. Crucially, we added reliability to the processing of the digit by implementing a control question after the spatial task, effectively turning the attentional cueing paradigm into a WM-task.

In the study of chapter II.3 'Irrelevant Arabic digits influence conscious perception during binocular rivalry', we reversed the logic implemented in chapter II.2 and used a novel binocular rivalry paradigm (Disrupted Rivalry) to investigate whether the attentional modulation induced by number cues has an influence on stimuli that have been supressed from consciousness. Our hypothesis for this experiment was that the numerical cue would influence which of two laterally presented stimuli would return first after they both had been suppressed.

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II.1

Introductory report of pilot data:

The search for an attentional SNARC-effect

Dennis Croonenberg[1,2], Hannah Boeijkens[2], Christianne Jacobs[2], Felix Duecker[2], Alexander Sack[2], Romain Martin[1] & Christine Schiltz[1]

1 Université du Luxembourg, Faculty of Language and Literature, Humanities, Arts and Education, ECCS, Esch-Sur-Alzette, Luxembourg

2 Maastricht University, Faculty of Psychology and Neuroscience, Department of Cognitive Neuroscience, Maastricht, The Netherlands

Abstract

The current study describes three pilot-experiments that attempted to replicate an attentional SNARC-effect as described by Fischer, Castel, Dodd, and Pratt (2003) and Dodd, Van der Stigchel, Leghari, Fung, and Kingstone (2008) that were initially set up to investigate an influence of stimulus-duration on spatial attention associated with number cues (e.g. Attentional STARC effect (Vallesi, Binns, & Shallice, 2008)). Interestingly, none of the experiments showed an attentional SNARC-effect despite strict matching of stimuli and procedure to those described by Fischer.

Introduction

Posner (1980) described the modulation of spatial attention towards the left and right due to exogenous (flashing of a location to the left or right of fixation) or endogenous (central arrows pointing towards the left or right) cues. An alternative to the presentation of central arrows as an endogenous cue is the use of Arabic digits that are known to shift attention towards the left for low numbers and towards the right for high numbers (Dodd et al., 2008; Fischer et al., 2003). The cueing of spatial attention due to Arabic digits has been conceptually linked to the observation that people tend to react faster with their left hand to low numbers and faster with the right to high numbers, an effect that is better known as the spatio-numerical association of response codes (SNARC) effect (Dehaene, Bossini, & Giraux, 1993). In reference to the SNARC effect the visuo-spatial attention cuing associated with numbers is thus also termed the attentional SNARC effect. An effect that is similar to the SNARC-effect is the STARC-effect (spatio-temporal association of response codes) and occurs when people have to categorise durations of stimuli as long or short. In this case, people react faster with their left hand to short (1s) stimulus durations and faster with the right hand to long (3s) durations (Vallesi et al., 2008).

The current experiments were set up with the intention to investigate whether a shift of visuo-spatial attention similar to the results of Fischer et al. (2003) also occurred for the duration of presented stimuli. In order to do this, we piloted several paradigms in order to replicate the initial findings, all of which failed to yield any results.

Methods & Results

Experiment 1:

5 right-handed volunteers (3 female 2 male, aged between 18 and 25) participated in the first experiment. Their task was to fixate on a fixation-cross presented on a 17" TFT-monitor while trying to detect a highly salient (bright green and round with high-contrast border) stimulus on the left or right side of space. Participants were instructed to respond via a button press on a numerical keypad using their right hand. This stimulus was presented in one of two boxes, which were placed on either side of fixation at approximately 3^{o} and spanned approximately 1^{o}. On a grey background 700ms before a target appeared,

participants were presented with a single Arabic digit (1, 2, 8 or 9) that was viewed passively and did not predict where the lateral green stimulus appeared. For this experiment we adopted 20% catch-trials, to ensure that participants were paying attention to the lateral targets and responded only in the presence of a stimulus. In total participants were presented with 480 trials, repeating each digit 100 times.

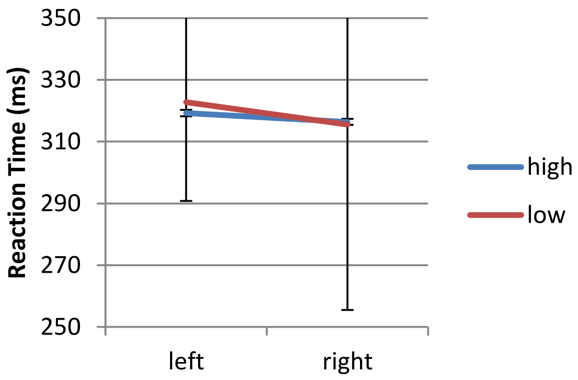

Figure II.1.1. Reaction times for experiment 1.

Results yielded an effect that was opposite to our expectations. People tended to be a bit faster in detecting stimuli on the right side of space when *the presented cue was of low* magnitude (315ms, SD: 53.2 vs 322ms SD: 55.4). Similarly, people were faster on the left side of space when the number was high (mean 316.35ms, SD: 49.3 vs 319.23ms, SD: 50.1). Comparing left- and right-handed reaction times between the presentation of high and low digits using a repeated measures ANOVA there was however no main effect of numerical magnitude on reaction time ($F(1,4)=.03$, $p=0.89$).

Experiment 2:

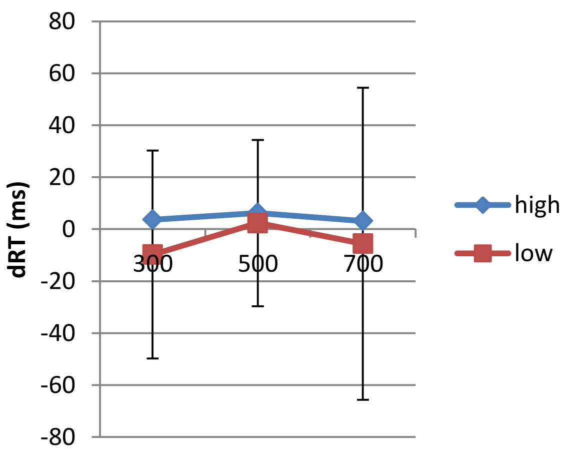

Figure II.1.2. dRTs for experiment 2 (right target minus left target) for different SOA's.

For the second experiment (n=8) we changed the stimuli to exactly match the size, position and colour of the stimuli used by Fischer et al. (2003) (5^o eccentricity, 1^0 width of box, 0.7^o width of white circle target). Furthermore, we adopted the use of three stimulus onset asynchronies (SOA) between cue and target (300, 500 and 700ms).

As can be seen in figure II.1.2, for each of the SOAs, differential reaction times (right minus left) yielded faster detections on the left side of space for the high numbers. The opposite was true for low numbers, indicating that participants were faster to detect targets on the right side of space after small digit cues.

Although participants did react faster to the left side of space for low numbers in the 500ms SOA, this did not differ from the high numbers (F(1,7)=2.15 , p=0.68). Averaged dRTs for the high numbers were 3.7ms (SD 31.2) 6.24ms (SD 40.3) and 3.17ms (SD 61.1)for SOA's of 300, 500 and 700ms respectively. For low numbers this was -9.7ms (SD 48.7), 2.34ms (SD 33.2) and -5.59ms (SD: 63.2).

Experiment 3

As we suspected that participants were ignoring the presented digit in the previous two experiments, we changed the task to incorporate an instruction which required participants to pay attention to a non-numerical aspect of the digit, namely its colour. For this experiment (n=14) both the central number and the lateral target could be either green or red. Participants were instructed to press a 1 on a numerical keypad with their right hand when the colour of the digit and lateral target matched and 2 if they did not match. Similar to experiment 2, we found that participants were generally faster to detect targets on the left side of space and that this was aided by the presence of high number cues, again finding a non-significant tendency opposite to the MNL-hypothesis (F(1,13)=1.31 , p=0.74). Averaged dRTs for the high numbers were 31.8ms (SD 45.5) -0.62 (SD 15.4) and 17.4ms (SD 18.0) for SOA's of 600, 800 and 1000ms respectively. For low numbers this was 14.7ms (SD 48.7), 1.54ms (SD 33.2) and -50.98ms (SD: 63.2).

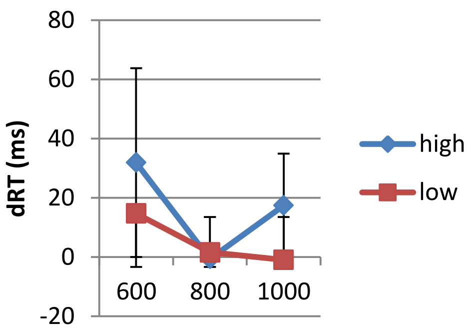

Figure II.1.3. dRTs (right minus left target) at different soa's for experiment 3

Discussion

The current experiments failed to replicate an attentional SNARC-effect in several attempts. It needs to be highlighted however, that the current study only describes pilot-data and therefore contains a low number of participants for the different experiments. Based on the average of effect sizes of both Fischer et al. (2003) and Dodd et al. (2008) a total amount of subjects of 31 would have been required (as is done by van Dijck, Abrahamse, Acar, Ketels & Fias (2014)), Although there are other studies that have reported not being able to find an attentional SNARC effect (Jarick, Dixon, Stewart, Maxwell, & Smilek, 2009; van Dijck et al., 2014; Zanolie & Pecher, 2014) studies that replicate or find similar effects are not hard to find (Dodd, 2011; Dodd et al., 2008; Galfano, Rusconi, & Umiltà, 2006; Goffaux, Martin, Dormal, Goebel, & Schiltz, 2012; Ranzini, Dehaene, Piazza, & Hubbard, 2009; Ristic, Wright, & Kingstone, 2006) begging the question why the current experiments failed to replicate. An obvious factor with regards to the current experiments is that it falls short in its sample size. This was due to their nature as a pilot for further investigation. As we were looking to find an optimal setting for replication we might have been too quick to decide on discontinuation and adaptation of an experiment.

In the first two experiments, as in Fischer et al, 2003 (and similar subsequent attentional SNARC studies) participants did not need to pay attention to the number cue itself, leaving the question open whether participants really processed the presented digit. Furthermore, for experiment 1 the target-stimuli were larger and eccentricity was smaller, potentially causing detection of stimuli to be significantly easier than the experiment by Fischer et al.(2003).

Although for the third experiment we changed the task to involve more active processing of the digit, this in itself might not have been sufficient to systematically induce number-space interactions. Since participants only had to pay attention to a presented colour, the numerical information of the digit was indeed of no importance to the task. A task on the colour of the number stimuli might not have caused enough number semantic processing for a spatial association to be activated. Alternatively, the judgment of colour-congruency might have interfered with the spatial processing as it required participants to make a left-right response (with their right hand, by pressing a 1 or 2 on the numerical keypad of a standard keyboard). In other words, the concurrent colour judgment task might have masked or overwritten any more subtle number-space interactions that occurred in parallel, but did not succeed in affecting participants' reaction time in this specific experimental setting.

In conclusion, although the current results did not yield an attentional SNARC-effect no inferences should be made on its existence or the reliability of earlier results in the literature.

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II.2

Masked Magnitude: The Influence of Masked Arabic Digits on Line Bisection

Dennis Croonenberg, Romain Martin, Christine SchiltzUniversité du Luxembourg, Faculty of Language and Literature, Humanities, Arts and Education, ECCS, Esch-Sur-Alzette, Luxembourg

Abstract

People portray a spatial bias during line-bisection tasks when lines are flanked by Arabic digits or when the lines are made of digits or number-words. This spatial bias is congruent with the magnitude of the presented number in that it causes a bias to the left for low numbers (1 & 2) and a bias to the right for high numbers (8 & 9). It is largely accepted that this occurs due to a spatial mental representation of numerical magnitude.

To investigate the effect of unconscious versus conscious processing of Arabic digits, we used both backwardly masked and unmasked trials during line-bisection. In masked trials the digit would be followed by a visual mask that surrounded the location of the digit. After the line-bisection, participants were asked whether they had perceived a target to check whether masking was successful. This was followed by a second question on the parity (Odd/Even) or magnitude (High/Low) of the number. Participants were instructed to give a guess on the magnitude or parity on trials in which they had not perceived the digit consciously.

We found that conscious processing (Seen Trials) would provoke a spatial bias in estimating the centre of a line that was congruent with numerical magnitude. Interestingly, this bias disappeared when the number was successfully masked. Even though participants would portray above-chance accuracy on the control-question, they did not show the spatial bias that would occur during seen trials.

Since there was no spatial bias in trials where participants answered correctly and that were also marked as ‘not seen’, we propose that the spatial bias induced by Arabic digits relies on conscious visual processing. Given the link between spatial bias and attentional modulation, future research might benefit from separating consciously and unconsciously processed Arabic digits.

Introduction

The presentation of Arabic digits is known to influence spatial tasks in several characteristic manners, which supposedly reflect the internal representation of numbers on a Mental Number Line (MNL) (Dehaene, Bossini, & Giraux, 1993). According to the MNL hypothesis people tend to make a mental ordering of numbers, going from left to right, where lower numbers are placed on the left and high numbers on the right, at least in western societies writing from left to right. A typical example of evidence for this cognitive phenomenon is the advantage in reaction times when responding to smaller numbers with the left hand and to larger numbers with the right in a parity judgment task (Dehaene et al., 1993). Furthermore, Fischer, Castel, Dodd, and Pratt (2003) showed that detection of lateral stimuli was speeded up when they were presented on the side that was congruent (e.g. Left for lower numbers and right for higher numbers) with the numerical magnitude of the passively viewed digit cues preceding the lateral target stimuli, indicating that there is also a visuospatial component to the number-space association, which is argued to be due to the modulation of spatial attention. As an alternative to the MNL hypothesis, it has been argued that this association between number and spatial laterality is related to the linguistic ordinal meaning of numbers as these tend to be learned in order of magnitude (Gevers, Reynvoet, & Fias, 2003, 2004). A second alternative concerns the verbal categorisation of numbers as 'high / low' or 'odd / even' where it is argued that the spatial association is due to the ad-hoc labelling of 'poles' depending on the task. Specifically, each ad hoc category is associated with a negative or positive pole and hence to a certain part of space (Proctor & Cho, 2009). However, due to the graded nature of certain tasks, where the more extreme values elicit stronger biases, this alternative fails to account for results in line bisection tasks. In line bisection tasks, subjects have to indicate the middle of a line, while it is flanked by Arabic digits or non-symbolic arrays of dots. Although the flanking numbers or quantities are irrelevant to the task, adults show a spatial bias towards the larger number, irrespective of its lateral position (de Hevia, Vallar, & Girelli, 2006; M. D. de Hevia & Spelke, 2009; Fischer, 2001b; Gebuis & Gevers, 2011). When participants were asked to bisect a line that consisted solely of numbers (e.g. 9999999) it was found that there was a bias towards the left for lines consisting of low numbers and to the right for lines composed of high numbers (Fischer, 2001a). Although Calabria and Rossetti (2005) did not find a spatial bias congruent with numerical magnitude when using this type of line, they did find an effect when the line was made up of written number words (e.g., the French equivalent of NINENINENINENINE). The spatio-numerical bias found during line-bisection can influence the visuo-spatial attention bias caused by hemi-spatial neglect (Bonato, Priftis, Marenzi, & Zorzi, 2008). Whereas people with left hemi-spatial neglect initially show a bias to the right when bisecting lines, this bias was modulated to the left for low numbers and to the right for high numbers when the written number-word version of the bisection task was used. Related results were found when asking people with hemi-spatial neglect to judge whether the middle number of three presented two-digit numbers was also the arithmetical middle of the three (For example 11_13_19). In this study, patients with neglect needed a higher numerical distance from the arithmetical middle than controls to classify it as being off, when the number was smaller than the arithmetical middle, indicating that the middle of a sequence was harder to determine for these people (Hoeckner et al., 2008). Taken together, the data strongly support the MNL framework. However, an interesting argument that goes against a spatial component in line-bisection influenced by numbers was made in a case-study by v van Dijck, Gevers, Lafosse, Doricchi, and Fias (2008) of a person with right-sided hemi-spatial neglect. This patient generally portrayed a spatial bias towards the left, but in number-line operations showed a bias towards the right, indicating a double dissociation. Moreover, Gebuis and Gevers (2011) also provide evidence that the line bisection bias that is supposedly due to numerical information in the study by De Hevia and Spelke (2009) might in fact stem from confounding visual information.

In the current experiment we aimed to elaborate on the nature of the dissociation between conscious visual information processing and spatial bias in a number line operation by implementing a single digit as an attentional cue during a computerized line-bisection task. Crucially, we added a backwards mask to diminish conscious processing of the attentional cue.

Classically, masking has been used to reduce the amount of processing of visual information to a point where participants no longer report on perceiving a stimulus, but are still able to report on characteristics of the stimulus at an above-chance level (Breitmeyer, Hoar, Randall, & Conte, 1984; Breitmeyer & Ogmen, 2000; Fry, 1934; Stigler, 1910) This is achieved by presenting two visual stimuli in close temporal proximity to each other, and many models have been made to explain this reduction in visual perception (For review see: (Bachmann, 1984; Breitmeyer & Öğmen, 2006; Breitmeyer & Ogmen, 2000; Francis, 2000)

We hypothesized that if masking would cause spatial bias to be diminished while the ability to correctly answer questions of parity or magnitude would remain intact, it can be concluded that spatial activation related to the processing of Arabic digits depends on consciously perceived visual perception.

Methods

Participants

A total of 41 right-handed volunteers (29 female, aged 21 +/- 2.3 years) participated in our study. All participants had normal or corrected to normal vision and received a monetary compensation for their participation. Participants were recruited via flyers and online advertisement from the student population at Maastricht University. All volunteers were required to provide written consent prior to the start of the experiment. The experiment was approved by the local medical-ethical committee at Maastricht University (METC).

Design & Task

The task was composed of viewing a numerical stimulus, which was followed by a line bisection task and a control question concerning the digit's numerical characteristics. At the start of each trial, participants were instructed to fixate on a cross at the centre of a 17" TFT-monitor at a viewing distance of 50cm. 200 pixels (53.4mm, 6.1^{o} visual angle) above the fixation cross a number (1, 2, 8 or 9) was shown for 40 milliseconds. The numerical stimulus and mask were placed eccentrically above the fixation cross to make masking easier but keep a horizontally central presentation. High (1, 2) or low (8, 9) numbers were repeated 32 times each (yielding 16 repetitions per individual digit and masking condition). Each participant completed a total of 128 trials.

1, 2, 8 and 9 were used as number cues in a low-contrast 7-segment layout (see figure II.2.1). Numbers were 50 pixels wide and 90 pixels high. In half of the trials, the number cue was followed by a mask with a stimulus-onset asynchrony (SOA) of 90 milliseconds. The mask was 100 pixels wide and 130 pixels high and consisted of a rectangular field of noise, which precisely surrounded the digit without overlapping.

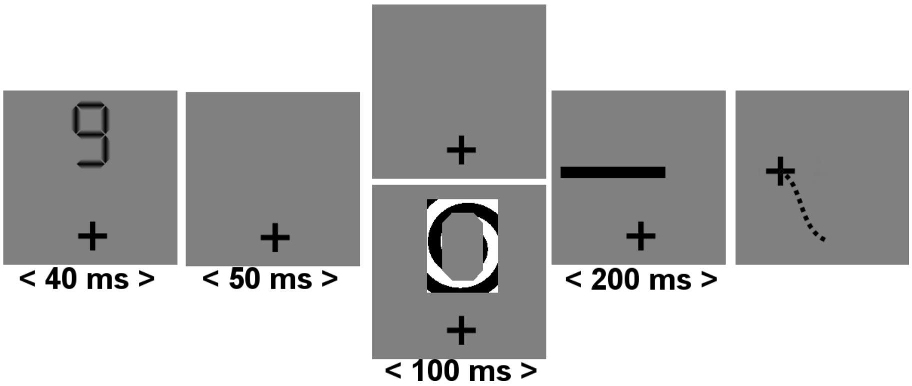

Figure II.2.1. *Procedure for the line bisection task. Please note that the contrast of the digit has been increased to enhance clarity. A one-digit number* (1, 2, 8 or 9) *was followed by a mask in 50% of the trials. After the mask (lower middle panel) or a blank period of similar duration (100ms, upper middle panel), a line was shown for 200ms. After the offset of the line, participants had to indicate via mouse- click where they had perceived the middle of the line.*

To investigate the spatial influence of the Arabic digits, digit presentation was followed by a line bisection task. A uniformly black, 10 pixels thick line was presented on the screen for 200ms. Directly after the line presentation, participants had to indicate where the middle of the line was situated, by mouse-clicking with their right hand on the position where they had perceived the line middle to be. We used three different line-lengths (400, 800 and 1200 pixels), whose middles were placed in 1 of 16 possible locations on the screen. After masked trials participants were asked to indicate using the left or right mouse-button whether they had or had not seen the number. All trials were terminated with a forced choice control question, asking either whether the number had been odd or even or whether the number had been low or high. For this question participants also had to indicate their answer using the left or right mouse-button. Either of the control questions occurred with a 50% likelihood.

Analysis

All trials where participants clicked beside the line were removed before subsequent analyses, resulting in the removal 15 trials in total. Moreover, we also discarded trials in which participants did not answer the control question correctly This entailed that for the unmasked condition 49 out of 820 trials were removed and 208 out of 820 for the masked condition. We further assessed whether performance on the control questions exceeded chance levels using one sided t-tests on mean individual count of correct answers.

In order to express the effect of numerical magnitude on spatial bias of bisection responses, we coded the spatial response biases as being congruent or incongruent with respect to the number cue magnitude. When the digit had a low magnitude (1, 2), deviations to the left were coded as a positive integer and deviations to the right as a negative integer that expressed the distance between the perceived vs. the real physical middle of the line in pixels. In contrast, for a high number (8, 9) a deviation to the right was coded as positive and a deviation to the left as negative integer. Consecutively, we then used a one-sided t-test to assess whether this congruency-measure differed from zero for those trials where participants (a) indicated to not have seen the digit (i.e. where masking was successful) and (b) correctly answered the control-question.

We performed a 2 x 2 repeated measures ANOVA on mean amplitudes of the deviations from the centre of the line. The design comprised digit magnitude (low/high) and mask (unmasked/masked) as within-subject factors. Separately for each masking condition, we also conducted a linear regression analysis of deviation during the line bisection task as a function of number magnitude (1, 2, 8 or 9).

Results

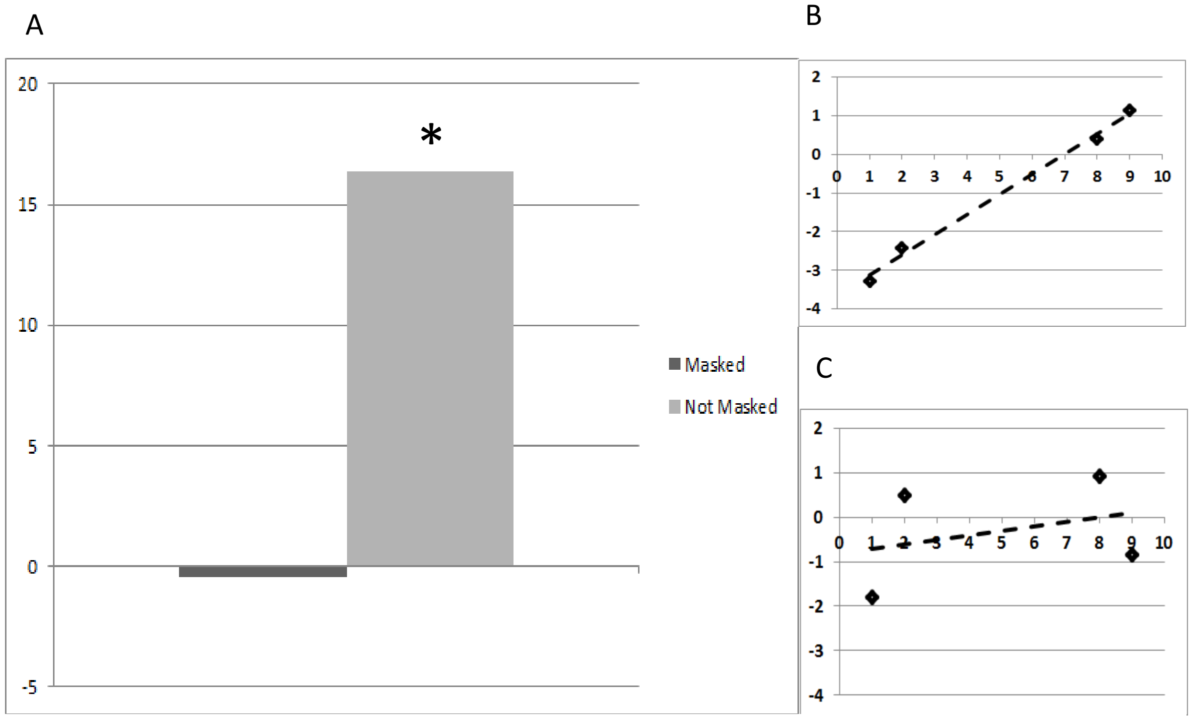

Figure II.2.2. A) Congruent spatial bias portrayed during line bisection-task for Masked and Unmasked trials. dRt B) linear regression of bias in unmasked trials. C) linear regression of bias in masked trials.

Congruency measures of the spatial bias congruency revealed a significant deviation from zero in the unmasked (t(40)= 2.01 , p=0.01) but not in the masked condition (t(40)= 0.301, p=0.76) when taking trials in which participants answered the control-question correctly. Consequently, these two conditions also differed significantly from each other (t(40)= 3.3, p<0.01). This indicates that there was no detectable spatial bias when participants did not consciously perceive the number cue (but still were able to correctly answer questions pertaining to the numbers' magnitude or parity). This contrasts with the unmasked condition, in which participants' bisection response was influenced by the magnitude of the Arabic digit cue. A 2x2 repeated measures ANOVA on mean amplitudes of the deviation from the centre of the line also showed a significant main effect of digit magnitude on the amplitude of the deviation ($F(1,40) = 8.089$; $p < 0.01$), such that deviations were larger when line bisection followed large digit cues (i.e. 8, 9) compared to small ones (i.e. 1, 2). Masking had no effect on the deviation ($F(1, 40) = 0.083$; $p = 0.774$). There was no significant interaction between mask and magnitude (Mask * Magnitude: $F(1, 40) = 0.012$; p

= 0.476). Accuracy in parity or magnitude was not affected differently due to the masking (Mask * Task (F(1,40) = 0.53, p = 0.26);

In the linear regression analyses (implemented separately for each masking condition) deviation in the line bisection task varied linearly as a function of number –cue magnitude in the unmasked condition. A significant linear fit was obtained due to the fact that bisection deviations tended more towards the right/left with small/large numbers respectively ($F(1, 2) = 340.96$; $p < 0.01$; $r^2 = 0.992$). In the masked trials, in contrast, bisection deviation did not vary as a function of number-cue magnitude ($F(1, 2) = 1.22$; $p = 0.68$, $r^2 = 0.525$). For both the masked and unmasked condition, performance in the control question on the number-cue characteristics was above chance (Masked accuracy = 73% correct, t(40)= 1.81, p = 0.04, Unmasked accuracy = 84% correct, t(40=3.58, p=<0.01).

Discussion

In the current experiment we investigated whether a spatial bias on line-bisection was influenced by prior presentation of single digits that had to be held in working-memory. Furthermore, we tested whether this bias was affected by the presence or absence of a backwards mask. Conforming to our expectations, we observed that the numerical magnitude of Arabic digits induced a spatial bias the left for low numbers and to the right for high numbers when there was no mask present. Critically, this bias disappeared when the digit was successfully masked, while the participants' ability to answer questions on the digits' parity or magnitude remained intact. We believe this is an indication that numerical semantic information can to some degree be dissociated from the spatial processing associated with Arabic digits.

The present results offer an intriguing addition to the discussion on the nature of a mental number-line representation that could potentially influence line-bisection. When the number-cue was masked, participants were still able to report on parity or magnitude of the presented digit when forced to do so, even though they indicated that they did not perceive a stimulus. This leads us to conclude that the processing for the latter type of semantic number judgment is to a certain extent unaffected by the mask. In contrast, masking the digit cue cancelled the spatial bias in the line bisection task, indicating that the processing which causes a spatial bias has been suppressed by the mask. This demonstrates that the nature of parity and magnitude processing is qualitatively different from the activation of spatial processes induced by number symbols.

Gevers, Ratinckx, De Baene, and Fias (2006) argue that the SNARC effect could be dependent on a dual-route architecture. They state that the effect might arise from a fast unconditional route that primes the response associated with the stimulus, while a slow conditional route will identify the response required by the task at hand. In case of the SNARC-effect this would imply that when the magnitude information (fast route) and conditions for the task instruction (slow route) converge, it causes a facilitation of the effector. The current result, however, does not entail a classical SNARC-effect but it is similar in its hypotheses with regards to spatio-numerical associations. When looking at the current experiment in the light of a dual-route architecture, it could be that the magnitude information causes a bias in the motor-movement that participants have to make and therefore has no reason to combine resources with the magnitude or parity information that is required by the task. Alternatively, it could be that the numerical information modulates attention to the left or right, and this is interfered with when the number is successfully masked (Fischer et al., 2003).

The fact that spatial representations which are activated by numbers are affected by the presence of a mask begs the question whether spatio-numerical associations are dependent on conscious processing. The global neuronal workspace hypothesis states that consciousness arises when incoming information is made globally available to multiple brain systems through a network of neurons. (Baars, 1993; Dehaene & Changeux, 2003, 2011; Dehaene, Kerszberg, & Changeux, 1998; Dehaene & Naccache, 2001). In the light of this framework our results could be interpreted as reflecting the necessity of consciously processing the number cue in order for it to exert an influence over the visuo-spatial attentional systems. These systems in turn affect the spatial performance and create a bias in the line-bisection task. In other words, a widespread activation of the numerical information is required before its magnitude is linked with a spatial position and this linking is required for attentional bias to occur. In short, the current results indicate that masking might obstruct the spatial processing that is generally regarded as an automatic activation that seems to come with the processing of Arabic digits.

Hubbard, Piazza, Pinel, and Dehaene (2005) claim that people are generally not aware of the association between space and numerical magnitude, implying that the relationship is in itself a subconscious one. In the logic of the before mentioned argument this would imply that conscious processing of numerical information is required to make an subconscious association have an influence over the processing of space (e.g. a bias in line-bisection). If this is the case, a valid inference would be that a wide-spread availability of (conscious) information causes subconscious parts of a network to be activated as well.

In summary, the current experiment offers an interesting approach to the subject of spatio-numerical associations. By implementing varying degrees of processing due to masking we were able to create two levels of spatial bias, offering a new way of studying it. In order to further investigate the difference between the processing of semantic labels of parity/magnitude associated with numbers and their spatial correlates future studies could attempt to focus trying on to diminish the degree to which a numerical stimulus is processed by making use of for instance Transcranial Magnetic Stimulation, Transcranial Current Stimulation or other ways of suppressing conscious processing.

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II.3

Irrelevant Arabic digits influence conscious perception during binocular rivalry

Dennis Croonenberg[1,2], Tom de Graaf[2], Alexander Sack[2], Romain Martin[1], Christine Schiltz[1]

1 Université du Luxembourg, Faculty of Language and Literature, Humanities, Arts and Education, ECCS, Esch-Sur-Alzette, Luxembourg

2 Maastricht University, Department of Cognitive Neuroscience, Vision and Awareness Lab, Maastricht, The Netherlands

Abstract

The magnitude of Arabic digits is known to affect visuo-spatial attention towards the left or right. Specifically, it can aid in detection or discrimination when the side where a lateral stimulus is presented is congruent with the numerical magnitude (left and lower than 5, right and higher than 5.

The current experiment makes use of a novel paradigm with regards to conscious perception, using binocular rivalry to supress conscious perception of two lateral stimuli for up to several seconds. In three separate experiments, we asked participants to report on the return of a stimulus on the left or right side of space after they had been supressed using a Disrupted Rivalry setup. Consecutively, participants had to report on the magnitude or parity of the presented number-cue.

Both the proportions of first return and reaction-times were affected by the magnitude presentation of central digits on the expected side of space. From this we propose that the spatial correlates that are associated with the attentional SNARC-effect have an influence on early visual processes such as binocular rivalry.

Keywords: Binocular rivalry, DRE effect, Numerical Cognition, Consciousness, Attentional SNARC effect

Introduction

The mental number-line hypothesis proposes that humans (in western cultures) represent numbers as going from left to right with an overall higher precision dedicated to small than to large numbers. Evidence for the existence of a left-to-right oriented mental number line was provided by the seminal paper of Dehaene, Bossini, and Giraux (1993), who found that people respond faster with their left hand to lower numbers and faster with their right hand to higher numbers when performing a judgement of the digits' magnitude or parity. This spatial-numerical association of response codes (SNARC) effect has given rise to the idea that the magnitude of a number is paired with task-dependent automatic activations that will aide or interfere with performing spatially lateralized tasks. In case of the SNARC-effect, the automatic activation of numerical quantity information is thought to have an influence on motor preparation involved with response selection for the specific tasks. This occurs because these tasks require a left/right lateralized response to numerical stimuli (Daar & Pratt, 2008; Gevers, Ratinckx, De Baene, & Fias, 2006; Ishihara et al., 2006; Keus, Jenks, & Schwarz, 2005).

Number-space compatibility effects have also been reported in attentional paradigm using Arabic digit as attention cues (and are termed attentional SNARC). It has indeed been shown that the automatic activation caused by numerical magnitude of passively viewed central non-predictive numbers can redirect covert attention according to numerical magnitude of the cue (Dodd, Van der Stigchel, Leghari, Fung, & Kingstone, 2008; Fischer, 2001; Fischer, Castel, Dodd, & Pratt, 2003; Galfano, Rusconi, & Umiltà, 2006; Hoffmann, Goffaux, Schuller, & Schiltz, 2016; Ristic, Wright, & Kingstone, 2006; Schuller, Hoffmann, Goffaux, & Schiltz, 2015; Zorzi, Priftis, Meneghello, Marenzi, & Umiltà, 2006).This is thought to occur in a similar manner to centrally presented non-predictive symbolic automated cues (such as left or rightwards pointing arrows or eye gaze) which are known to aid or interfere with detection or classification of stimuli presented on the spatially compatible side (Galfano et al., 2012; Ristic & Kingstone, 2012). In other words, numerical magnitude of centrally presented Arabic digits is known to affect visuo-spatial attention. Specifically, attention is drawn to the left for low numbers and to the right for high numbers.

This manipulation of covert attention by passively viewed numbers (or attentional SNARC-effect) is thought to have an effect on early visual processing. For instance, activity in the early visual cortex is increased when the magnitude of a centrally presented Arabic digit is congruent with the appearance of a lateral target (Goffaux, Martin, Dormal, Goebel, & Schiltz, 2012; Schuller et al., 2015). Furthermore, when TMS is applied to the early visual cortex, number-primes increase perception of phosphenes on the contralateral hemisphere associated with the magnitude of the numerical prime (Cattaneo, Silvanto, Pascual-Leone, & Battelli, 2009).

Binocular rivalry

One of the prime functions of the early visual cortex is to integrate the images coming from both eyes in order to perceive depth. However, when non-matching stimuli are simultaneously presented to the individual eyes (i.e., a house to the left eye and a face to the right) the information is not integrated but alternates in consciousness (Alais & Blake, 2005; Blake, 1989; Wade & Wenderoth, 1978). This particular phenomenon is referred to as binocular rivalry and has been the subject of an extensive amount of research.

One of the core strengths and interests of binocular rivalry experiments is their ability to manipulate conscious processes (Blake, 1997; Crick & Koch, 1995; Logothetis, 1998). Which stimulus or eye is dominant and which is suppressed can be controlled using several approaches. One method involves letting one eye adapt to a stimulus for a short time and consecutively presenting the other eye with a contrasting stimulus, which results in a suppression of the first image (flash-suppression) (McDougall, 1901; Tsuchiya, 2008; Wolfe, 1984). The duration of flash suppression has been shown to depend on local spatial processing where some parts of visual space return the initial stimulus back to consciousness sooner than other parts (van Ee, 2011). It is also possible to suppress stimuli from consciousness for extended periods of time by presenting one eye with a stable stimulus while the other eye is stimulated with a high-contrast stimulus that changes continuously, resulting in a prolonged suppression of the stable stimulus (Tsuchiya & Koch, 2004, 2005; Yang & Blake, 2012; Yuval-Greenberg & Heeger, 2013). A phenomenon that has only recently been described in detail involves the suppression of a stimulus from visual consciousness for a surprisingly long period by presenting a rivalling stimulus to the other eye for only a short amount of time. Similar to flash-suppression, this Disrupted Rivalry Effect (DRE) is achieved by first presenting a monocular stimulus and following this up with a rivalling stimulus on the other eye. However, when the rivalling stimulus is removed again shortly after its onset it results in a suppression of the initial stimulus from consciousness, causing the only (monocular) visual stimulation to be invisible for periods lasting up to three seconds (De Graaf, van Ee, Croonenberg, Klink & Sack, in review).

It has been established that binocular rivalry is resolved by cross-inhibiting monocular channels at an early visual level (Brascamp, Van Ee, Noest, Jacobs, & van den Berg, 2006; Lansing, 1964; Stollenwerk & Bode, 2003). For instance, when macaque-monkeys were presented with conflicting gratings, the primary visual cortex (V1) and the secondary visual area (V2) of the extra-striate cortex revealed activity that corresponded to the switching between precepts (Leopold & Logothetis, 1996). Accordingly, activation levels for these visual areas dropped between 48% and 77% in humans when comparing functional Magnetic Resonance Images (fMRI) signals of dominant and suppressed gratings (Lee & Blake, 2002). However, the effects of binocular rivalry are not restricted to early visual areas. When using complex stimuli, such as houses and faces, higher order regions such as inferior parietal sulcus and the fusiform face area depict lowered activity when suppressed during binocular rivalry (Tong, Meng, & Blake, 2006).

Attention and Binocular rivalry

Attention can influence binocular rivalry in several ways. First, when both competing stimuli have a simultaneous onset, attention biases which stimulus is perceived first by favouring the attended stimulus (Chong, Tadin, & Blake, 2005; Ooi & He, 1999). This also applies to endogenous and exogenous cues when used in similar fashion as for spatial cueing, such as arrows pointing towards the left or right (Chong & Blake, 2006; Mitchell, Stoner, & Reynolds, 2004). However, when rivalry is already on-going, the matter becomes more complex. Some authors only find a very limited influence of attention on the perceived dominance periods, while others report that the dominance of the attended stimulus can be prolonged (Helmholtz, 1925; Lack, 1978; Meng & Tong, 2004; Meredith & Meredith, 1962; van Ee, Van Dam, & Brouwer, 2005). Chong et al. (2005) made an attempt to resolve this controversy by proposing that it is the attention to rivalry-relevant stimulus features in a task that is of importance to the influence on duration, whereas the generic instruction to focus attention on a stimulus would not be sufficient to induce attentional modulation of the rivalry period duration. By giving participants the instruction to report on subtle continuous changes in the shape or brightness of a stimulus Chong et al. (2005) were thus able to lengthen the period in which the attended stimulus was dominant. Similarly, when attention was drawn to a demanding distractor task that was presented at the same time, but did not visually interfere with the rivalry, switching between percepts slowed down (Paffen, Alais, & Verstraten, 2006).

The effect of attentional cueing on DRE as used in the Posner-paradigm or the Attentional SNARC-effect is currently unknown. The current study was set up to investigate if number cues have an effect on early visual processing to such an extent that they can influence durations of suppression in binocular rivalry. By adopting DRE in a task where Arabic digits are used as a spatial cue we expected numbers to shift attention towards left or right based on numerical magnitude and consequently causing a faster return of the supressed stimuli on that side of space.

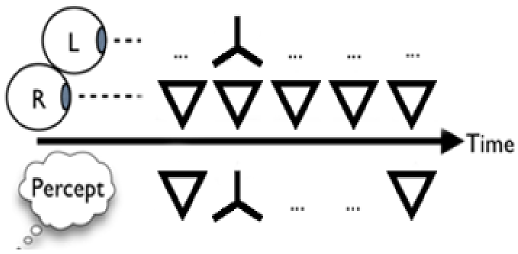


Figure II.3.1: *Disrupted Rivalry Effect. When a monocular stimulus is supressed by a rivalling stimulus that is removed after a short amount of time it will result in a suppression of the initially presented stimulus for a prolonged period.*

Methods

Participants

72 right-handed volunteers (56 female, aged 21 +/- 2.4) participated in the study (24 for each of the three experiments). All participants had normal or corrected to normal vision. For the first experiment subjects partook in two identical sessions lasting half an hour each with a period of at least 48 hours between sessions. The second and third experiment consisted of only one session. Participants received a monetary compensation. All participants provided written consent prior to the start of the experiment. The current experiment was approved by the local medical-ethical committee at Maastricht University (METC).

Materials

Visual stimulation was offered using a custom-built Wheatstone-stereoscope (Wheatstone, 1838) and two identical 17” TFT-monitors to ensure different images being received by each eye. Stimuli were presented using Presentation software (Neurobehavioral Systems, CA, USA). In order to prevent binocular rivalry occurring outside of the borders of the monitors, the experiment took place in a darkened room. Participants had to respond by pressing either “z” or “/” on a generic keyboard with US-International layout (experiment 1 & 2) or give a vocal response (experiment 3).

Design & Task

Experiment 1 - Direct response codes:

The current study made use of DRE to measure the influence of number cues on the orienting of attention towards the left or right side of the visual field. Each experimental trial consisted of 4 phases. In the first phase (adaptation), two stimulus elements (either stars or triangles) were presented to one eye and remained on screen for the remainder of the trial. The elements were placed 6.221 degrees towards the left and right of a central fixation. Either 100 or 500ms after onset of adaptation, the central fixation-cross was replaced by an Arabic digit (1, 2, 8 or 9) for 300ms.

1000ms after onset of adaptation, the eye not receiving the adaptation-stimulus was presented with a rivalling stimulus. If the adaptation-stimulus contained a triangle the rivalling stimulus was a star and vice versa.

300ms after its onset the rivalling stimulus was removed, which resulted in a prolonged suppression of the adaptation-stimulus (Dark period/ DRE-effect). Participants were instructed to indicate which of the stimulus-elements (left or right) returned first to their conscious perception as fast and accurately as possible. Responses were given by using the left (left stimulus returned first) or right (right stimulus returned first) index finger.

To ensure that the number-cue had been perceived and remembered correctly, participants had to indicate via button-press whether the number was even/odd (parity) or higher/lower than 5 (magnitude) after each trial. Parity- or magnitude-questions were equally likely to occur. Participants were not informed which question would be presented, to ensure that they would keep the single digit in working-memory and not the answer to the question. Trials were separated by a 1500ms inter-trial interval and four breaks were built into the program after each block of 80 trials, in order for participants to rest their eyes. Visual stimuli were accompanied by a background grid that remained on screen throughout the experiment. Stimuli were 2.7 visual degrees (27.7mm) in size and were placed 6.221 visual degrees (61.41mm) away from fixation.

Which eye received the adaptation-stimulus was randomly counterbalanced between trials. The complete design was composed of 2 adaptation positions (left/right eye), 2 stimulus positions (triangle on the left and star on the right or vice versa), 2 SOAs (100ms, 500ms after onset of adaptation) and 4 number-cues (1,2 ,8 ,9) resulting in 32 different types of experimental trials. Each of these trials was mirrored by a control-condition in which the number cue was replaced by a “[ ]” which was chosen for its symmetry and lack of spatial association (as used in Goffaux et al, 2012). During these trials the magnitude or parity task was removed. Each condition was repeated 5 times per session resulting in a total of 640 trials per participant over the two sessions.

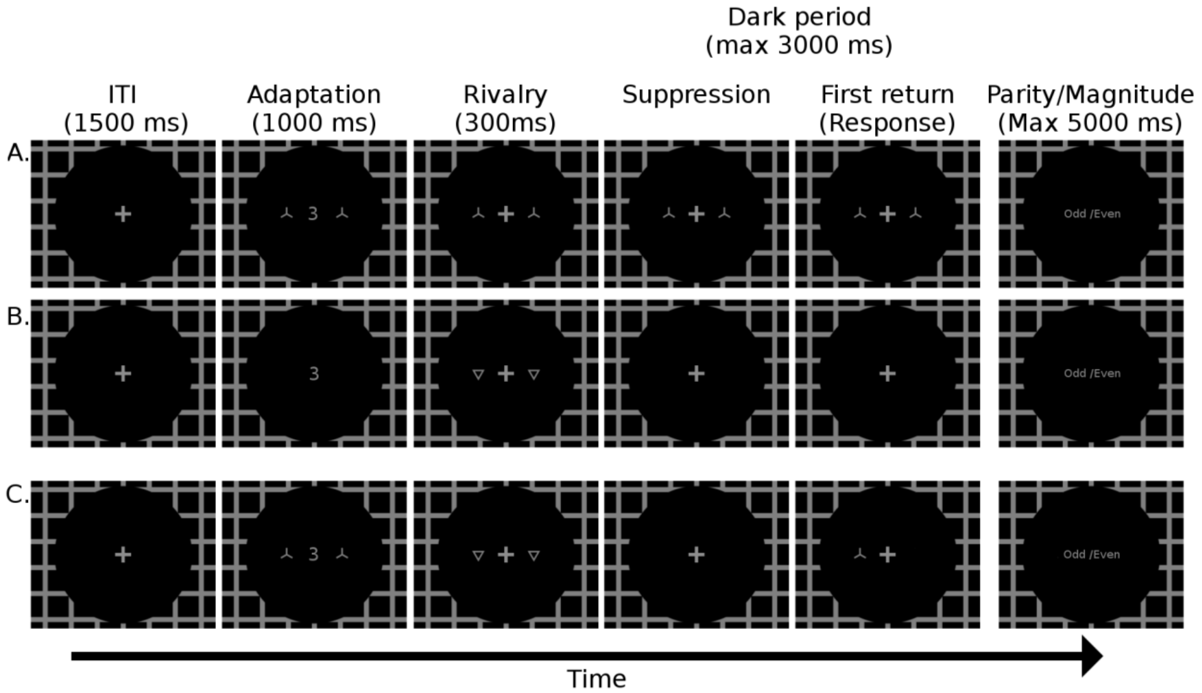


Figure II.3.2. *Procedure of an experimental trial (fixation and number-cue are not drawn to scale). A) Stimulation-procedure for the eye receiving the adaptation-stimulus. B) Stimulation-procedure for the eye receiving the rivalling stimulus. C) Conscious Percept. During the adaptation-phase only one eye is stimulated and allowed to adapt. The number cue is presented during the adaptation-phase to both eyes (100 or 500ms after onset of stimulus-elements). After 1000ms a rivalling stimulus is offered to the opposing eye, causing this eye to gain immediate dominance. Removing the rivalling stimulus causes the participant to experience a dark period in which the remaining stimulus elements are temporarily not consciously perceived. Participants have to indicate which stimulus element returned first (left or right of fixation) and subsequently do a magnitude or parity judgment on the number cue.*

Experiment 2 - Reversed response codes:

To ensure that results were not biased by motor preparation, we conducted a control experiment containing the same parameters and stimuli as experiment 1, but differing in the response requirements. Here, participants were instructed to use their right hand when the stimulus on the left returned first and their left hand for a first return on the right. A second difference was the removal of SOA as an extra condition, since only the 500ms delay of digit-onset after onset of adaptation was used.

Experiment 3 - Vocal Responses:

In the third experiment all parameters were the same as in experiment 2, except that participants were asked to indicate verbally which type of stimulus had returned first instead of indicating their position (e.g. triangle or star). Moreover, contrary to experiment 1 and 2, two different shapes were presented during the adaptation phase, that consisted in a triangle left of the fixation and a star on the right, or vice versa. After suppression of both these stimuli with the contrasting stimuli on the other eye (briefly inducing the opposite concept, i.e. left star and right triangle or vice versa), participants were instructed to respond vocally with either 'ti' or 'to' for triangle or star respectively, to indicate which shape was returning first. The association of the vocal response with a certain shape was counter-balanced between participants.

Analysis

Trials in which participants did not respond or gave a wrong answer on the magnitude or parity-task were excluded resulting in the removal of 903 out of 8600 total trials for experiment 1, 755 out of 4300 for experiment 2 and 667 out of 4300 for experiment 3 . For all three experiments, proportion of responses (proportion of left-first responses) dependent on digit cue where analysed using repeated measures GLM in order to quantify effects of numerical magnitude. The neutral [] cue was coded as having the numerical value 5. Differential Reaction Times (dRTs) were calculated (RT(first return on the right) minus RT(first return on the left)) and analysed with repeated measures GLM. In the first experiment SOA was also taken into account as an extra factor with two levels (150 and 500ms). To express the directionality of the effects of digits, linear regressions were fitted to the values of dRT and proportions of responses as a function of digit cue magnitude.

Results

Experiment 1

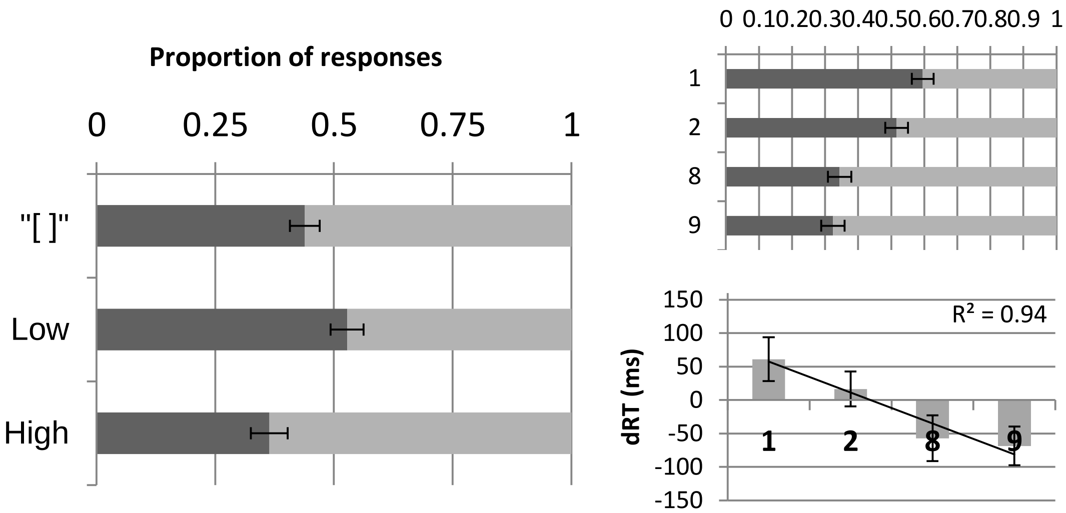
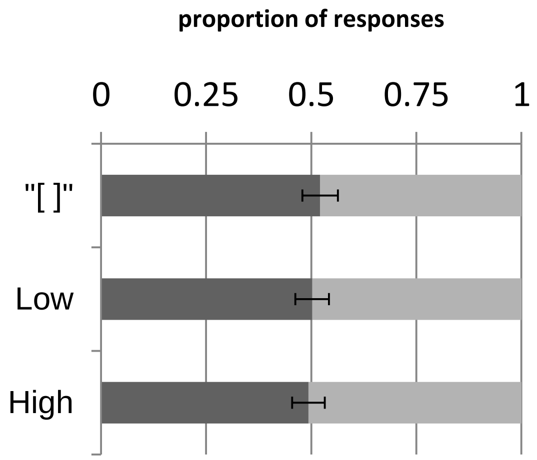


Figure II.3.3. Results of experiment 1. A) Proportions of left-first (dark-grey) and right-first (light-grey) responses for the magnitudes of presented Arabic digits (low and high) and the control condition ("[ ]"). B) Proportions of left- and right-first response for individual digits. C) Differential reaction times (right minus left) for the four Arabic digits used.

In our first experiment the average proportion of left responses was 0.52 (SD=0.19) for low numbers, 0.36 (SD=0.19) for high numbers and 0.42 (SD=0.16) for the neutral '[ ]'-stimulus. For individual numbers averaged dRT were 61ms (SD=16ms), 16ms (SD =12.7ms), -57ms (SD=16.8ms), -68ms (SD=14.2) for 1,2,8,9 respectively and 23ms (SD=12.1ms) for the numerically neutral cue'[ ]'. Numerical magnitude had a significant effect on proportions of responses (F(2,23)=10.099, p<0.001) and dRT (F(2,23)=4.460, p=0.05). Linear regression showed that the proportion of left vs. right responses was predicted by the numerical magnitude of the digit cue, showing a significantly negative slope (F(1,2) = 87.272, p=.011) with r^2=0.97 indicating a decrease in left-first responses when the numerical magnitude increases. For dRT we found a similar negative slope (F(1,2) = 48.152, p=0.02) with r^2=0.94. For the current experiment no interaction between magnitude and SOA was found for both proportions (F(2,23)=0.9, p=0.91) or dRT (F(2,23)=0.9, p=0.74). SOA portrayed no main effect (F(2,23)=0.87, p=0.90).

Experiment 2



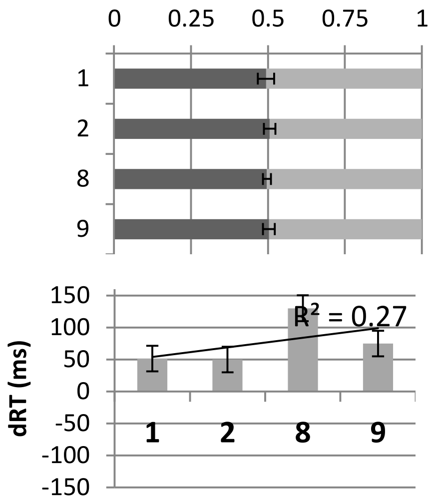


Figure II.3.4. Results of experiment 2. left) Proportions of left-first (dark-grey) and right-first (light-grey) responses for the magnitudes of presented Arabic digits (low and high) and the control condition ("[ ]"). Top-right) Proportions of left- and right-first responses for individual digits. Bottom-right) Differential reaction times (right minus left) for the four Arabic digits used.

For the second experiment the average proportion of left responses was 0.49 (SD = 0.15) for low numbers, 0.50 (SD=0.17) for high numbers and 0.47 (SD=0.16) for the neutral '[ ]'-stimulus. For individual numbers averaged dRT were 51ms (SD = 16ms), 49ms (SD =12ms), 130ms (SD=14.2ms), 74ms (SD=12ms) for 1,2,8,9 respectively and -80ms (SD=10.2ms) for the numerically neutral cue '[ ]'. Numerical magnitude had no effect on proportions of responses ($F(2,23)=0.291$, $p=.88$) and dRT ($F(2,23)=0.192$, $p=0.16$). Linear fits also portrayed no significant influence of digit magnitude ($F(1,2) = 0.056$, $p=0.83$) with $r^2=0.03$ on proportions and dRT ($F(1,2) = 0.53$, $p=0.84$) with $r^2=0.03$.

Experiment 3

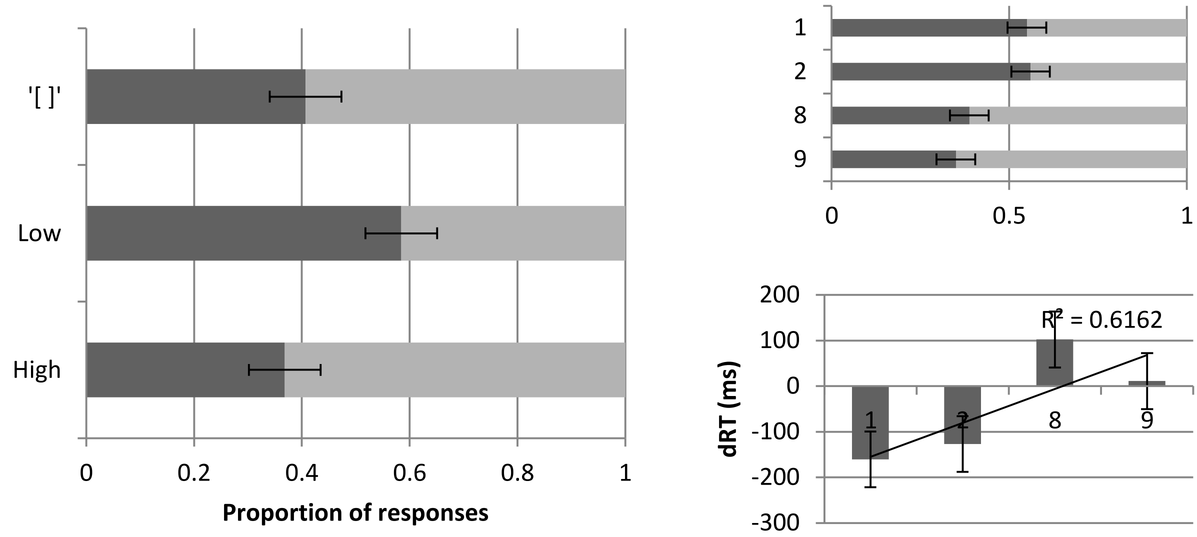


Figure II.3.5. *Results of experiment 3. left) Proportions of left-first (dark-grey) and right-first (light-grey) responses for the magnitudes of presented Arabic digits (low and high) and the control condition ("[ ]"). Top-Right) Proportions of left- and right-first responses for individual digits. Bottom-right) Differential reaction times (right minus left) for the four Arabic digits used*

For the third experiment the average proportion of left responses was 0.58 (SD=0.13) for low numbers, 0.37 (SD=0.14) for high numbers and 0.40 (SD=0.10) for the neutral '[ ]' stimulus. For individual numbers averaged dRTs were -160ms (SD=16ms), -127ms (SD=12ms), 102ms (SD=15ms), 11ms (SD=13ms) for 1,2,8,9 respectively and -159ms (SD=10.2ms) for the numerically neutral cue '[ ]'. Numerical magnitude had an effect on averaged proportions of responses ($F(2,23)=8.950$, $p<0.001$) and dRT ($F(2,23)=10.806$, $p<0.01$). Proportions of left vs. right responses portrayed a linear decrease as a function of magnitude increase ($F(1,2) = 28.04$, $p=0.034$ and $r^2=0.90$), while dRT revealed no such linear trend ($F(1,2) = 3.211$, $p=0.21$) with $r^2=0.61$.

Discussion

The present study explored whether attentional modulation induced by Arabic digits (e.g. Fischer et al. (2003)) can affect early visual processing. To this aim we combined the recently reported Disrupted Rivalry Effect (DRE) (de Graaf et al., in review) with attentional cueing effects caused by Arabic digits (e.g. Fischer et al., 2003; Hoffmann et al., 2015). After temporarily wiping out from conscious vision two lateral stimuli viewed in a binocularly rivalry set-up thanks to the DRE, participants had to indicate which of the two stimuli returned first to their conscious perception. Critically, a single Arabic digit was presented in the centre of the visual field before making the lateral stimuli disappear and participants had to remember the numerical information throughout the trial. In the context of this binocular rivalry paradigm, numerical magnitude of the digit systematically influenced the side on which stimuli were perceived to return first. Specifically, when participants had to remember the number 8 or 9, the amount of first-returns was higher on the right side of space, while the opposite pattern was observed for low numbers (i.e. 1 and 2) which enhanced perceptual reappearance of stimuli on the left side of space.

Given that binocular rivalry is known to be settled at an early stage of visual processing, the current results show that early visual processing can be influenced by the numerical magnitude of Arabic digits. In line with previous literature on spatial cueing it seems that the digits act as symbolic automated spatial cue which draw attention towards the hemi-field that is congruent with their magnitude (Dodd et al., 2008; Fischer et al., 2003; Goffaux et al., 2012; Ranzini, Dehaene, Piazza, & Hubbard, 2009; Salillas, El Yagoubi, & Semenza, 2008). In our binocular rivalry setting, this in turn causes faster return of the suppressed stimulus on the corresponding side of space.

The most striking results were obtained in the first experiment, where subject signalled left/right stimulus returns with the left/right hand, respectively. Indeed the proportions of left- or right-first responses were fully in line with our hypothesis that low numbers would cause more occurrences of left-first responses and high numbers would induce more right-first responses. Remarkably, the neutral '[ ]'-stimulus elicited a proportion of left-first and right-first responses that fell in the middle of the two types of digit cues.

Even though the second experiment was unable to find an effect of numerical magnitude due to the reversed response codes, when results were combined with the first experiment the effect of magnitude on proportions prevailed.

The initial results by Fischer and colleagues (2003)(see also (Hoffmann et al., 2016)) indicated that effectiveness of attentional cues depended on the *SOA* between number-cue presentation and detection of a lateral stimulus. In *experiment 1*, where 2 different SOAs were used, we did not find any such influence on any of the 2 performance measures (i.e. proportions and RTs). This lack of SOA effect probably occurred because our task inherently differed from the one used by Fischer et al. (2003). First, it required participants to keep the digit in memory throughout the trial, potentially causing internal rehearsal, which in turn diminished the effects of SOA. This contrasts with the original task by Fischer et al. (2003) where the Arabic digits were passively viewed just before a lateral target detection task. A second difference factor might be the unpredictability of the DRE. As we only controlled when lateral stimuli disappeared, but not the duration until stimuli returned to participant's conscious vision (which was varying between trials and participants), the timing between onset of the central digit and return of the lateral stimulus percepts could not be manipulated as systematically as it is done in the studies reporting an effect of SOA.

Reaction times complemented the outcomes obtained with proportions for each of the four digits used in experiment 1. When a stimulus reappeared on the cued side of space, it did so faster than for the un-cued side in the setting of experiment 1 where participants were asked to signal the side of stimulus reappearance by pressing the response button on the corresponding side. Current results are similar to effects found by van Ee (2011) where parts of the visual field were shown to be able to release suppression faster than other parts. For his experiment, participants had individual parts of space that would return first more often, which was consistent over time. Similarly, the current results indicate that laterally oriented attention speeded up the process through which the attended part of the visual system overcomes inhibition.

To put it differently, not only did symbolic automated attentional cueing induced by numbers result in increasing the chance of stimuli on the cued side first returning to conscious vision more frequently, but numerical attention orienting also made the cued stimuli reappear faster.

In contrast, when reversing response instructions in experiment 2 (such that left/right-sided reappearance of stimuli had to be signalled with the right/left hand respectively) qualitatively different results than for experiment 1 were obtained and reaction-times and proportions of first-responses portrayed a different pattern. While in experiment 1 classical SNARC effects might have facilitated motor-preparation for the effector that was congruent with numerical magnitude, it is possible that the SNARC effect interfered with the numerical cueing effect in experiment 2. For instance, when the magnitude of the digit cue was low, number-space related compatibility effects could have caused motor preparation on the left side (Gevers et al., 2006; Ishihara et al., 2006), while the present binocular perception task in most instances required a response on the right side to signal that the stimulus first returned on the left. The incongruence between classical SNARC effects and the required motor-response in this task could have affected the results, such that number cues did not influence the proportion of left vs. right-sided stimulus appearance according their magnitude. It is also possible that the classical SNARC effect made people more prone to use the hand that was congruent to the numerical magnitude, making them less reliable in the judgement of the first return. To summarize, the current experiment seems to exemplify the well-known fact that numerical cues interact with both spatial attention and response codes (Dodd et al., 2008). In the first experiment we saw the effect of an attentional modulation that was intensified by its congruency with the SNARC-effect, yielding the strongest effects on reaction time and proportions of onset of the lateral stimulus. In the second experiment, the effect of response codes on numerical cues seemed to obstruct the attentional effects we observed in experiment 1.

In the third experiment participants did not respond using their hands, but gave vocal responses, eliminating the distortion that numerical magnitude might have on response codes. Furthermore, participants did not need to indicate a first return on the left or right side of space, but rather which stimulus type returned first, i.e. triangle or star, eliminating the need to think in terms of spatial location altogether. During the third experiment, the spatial effect on proportions prevailed. Therefore, we conclude that this experiment shows the attentional effect of numerical magnitude which is not influenced by motor-biases caused by the classical SNARC-effect.

The data describing the proportions of left vs. right-sided stimulus reappearance as a function of digit magnitude was extended by looking at the effects of individual digits 1, 2, 8 and 9. Given that only four digit-cues were used in the current experiment, interpretation of the linear regressions must be made with caution. However, the fact that there seems to be a consistent linear trend for proportions of stimulus reappearance might point towards a novel feature of numerically induced visuo-spatial attention orienting. In most studies that use Arabic digits as a spatial cue, there is only a report of high and low magnitude and/or congruency (Casarotti, Michielin, Zorzi, & Umiltà, 2007; Dodd, 2011; Dodd et al., 2008; Fischer, 2003; Ristic et al., 2006; Stoianov, Kramer, Umilta, & Zorzi, 2008). When interpreted as such, it is logical to conclude that a single category of spatial cues is associated with a single side of space in a similar way that arrows or gaze can be used to cue a spatial hemi-field. In this case, one would not expect differences between individual numbers to occur. When taking the logic of the current results to the end, it seems that not only does the digit draw attention to the left and right side of space, but it does so with a certain strength, creating stronger biases for 1 and 9 and weaker biases for 2 and 8. It remains to be answered if this is something that occurs due to the position of the stimuli being more congruent with the mental representation of more extreme digits 1 and 9, as proposed by the mental number-line hypothesis. An interesting alternative explanation would be that the cueing causes attention to have a certain amount of power when being pointed towards the locations where the stimuli occur.

The current experiment introduced a novel method for studying the effects of attentional cues using the DRE. We provided evidence that numbers can have an influence on processes involved with conscious visual awareness when used as automated symbolic attention cues. A question that remains to be answered is whether participants have a faster return of lateralized percepts due to a direct modulation of early visual processing, or whether they become more efficient to detect the return of visual stimuli on this side of space, suggesting an influence on later processes involved with visual perception. Nonetheless, we conclude that the use of binocular rivalry and DRE are excellently suited for further exploration of the nature of attentional cueing and consciousness. Furthermore, we propose that research which involves Numerical magnitude or ordinality in a spatial context could benefit from incorporating experiments that involve manipulating conscious processing. Especially if the salient effects are as clear as it is for DRE.

Given that in the current experiment we were able to find an effect on disrupted rivalry due to numerical magnitude we argue that specific types of visual processing are fundamentally affected by the presentation of Arabic digits. We believe that it is therefore imperative to investigate further in which ways parts of the visual scene are affected by the presence of numbers.

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Part III

The role of visuo-spatial working memory in Developmental Dyscalculia

"Our heads are round so thought can change direction"

- Allen Ginsberg

Introduction

The development of numerical and mathematical skills, as described in the introduction to this thesis, is not always a straightforward process. In order to grasp the concept of numerosity and make numerical or mathematical representation there are of course many type of individual differences that play a role including intellectual ability, general intelligence and socio-economic status. Developmental Dyscalculia (DD) is something that happens independent of these factors in about 3-6% of the population (Mareschal, Butterworth, & Tolmie, 2013; Shalev, Unit, Zedek, & Berlin, 2007) and describes the inability to perform mathematical operations at a similar level as that of peers while other intelligence-related capabilities are considered normal.

Problems with representing and understanding numerosity as well as an impairment in acquiring and retrieving arithmetic facts are two tendencies that seem to be at the core of this performance deficit (Butterworth, 2005). Recent research has shown that DD is often inherited and can persist into adulthood. A major interpretation existing in the literature today states that dyscalculia is due to a core deficit in representing and understanding numerosity (Butterworth, 2005, 2010; Butterworth et al., 2011). In order to handle and use numerals properly, their semantic (i.e. cardinal and ordinal) properties must be understood. In other words, the learner must develop a specific and robust mental representation of number magnitude and/or order that is systematically associated with the number symbol, when learning about it. Children with DD do not acquire these numerical representation in a typical manner, but they have problems in the mastery of a wide range of numerical concepts and skills such as counting skills, magnitude processing, arithmetic, transcoding between number words, digits and quantities and the spatial representation of numbers (Kaufmann, 2002; Landerl, Bevan, & Butterworth, 2004; McCloskey, Caramazza, & Basili, 1985; Price, 2008). Impairments in one or more domain-general skills like working memory or attentional processes can be another source of DD (Kucian & von Aster, 2015)

There is some discrepancy in the literature on whether and how dyscalculics are affected by deficiencies in WM. Several behavioural studies do not support the notion that WM plays a causal role in DD, because the performance of DD children did not differ from typical math-performers on forward and backward digit-span (Landerl et al., 2004), word-span or even visuo-spatial-tasks such as Corsi Block-tapping (Temple & Sherwood, 2002; Temple & Sherwood, 2002). Similarly, Hitch and McAuley (1991) argued that deficits in concurrent span counting tasks are the result of a counting deficit related to fluency of numerosity, rather than a WM deficit. Other studies, in contrast, did find lowered WM performance in participants with DD. For instance, it was observed by McLean and Hitch (1999) that whilst there were no effects on phonological WM-measures using non-numerical stimuli, the forward and backward digit span of a DD-group was reduced. This led to the conclusion that a DD-related impairment of WM was present, but did not include the phonological loop (McLean & Hitch, 1999).

There is however a part of the literature that shows no discrepancies. Although a deficit in phonological WM might be lacking, when specifically looking at visuo-spatial WM there is quite some evidence that an impaired VSWM contributes to the difficulty that DD participants are having on numerical and spatial tasks (Kucian et al., 2006; McLean & Hitch, 1999; Rotzer et al., 2008; Rotzer et al., 2009). The main function of VSWM is to produce and maintain an internal spatial representation of locations and stimuli. Its involvement in mathematical operations seems to lay in its ability to represent numerosities by placing them on a mental number-line but it can also aid in remembering digit sequences and schematically representing operational procedures by giving them relative positions in a mental space (Booth & Thomas, 1999; Hegarty & Kozhevnikov, 1999; KYTTÄLÄ, Aunio, & HAUTAMÄKI, 2010; Passolunghi & Mammarella, 2010)

The next chapter focuses on the VSWM capabilities of children with DD in an event-related fMRI paradigm and compares them to two control-populations (typically developing children and adults). For this experiment we were very meticulous in making sure that the two populations of children were matched in intelligence, age and verbal abilities. By offering both an arithmetic task (addition) and a VSWM-task (Corsi-derived) we were able to compare network-activations in both these tasks and make subsequent comparisons between groups in order to better understand how mathematical proficiency relates to visuo-spatial working memory and executive control processes. Concretely, we investigated how adults as well as children with and without specific learning difficulties in mathematics deploy executive control processes in the context of a VSWM task. The experimental paradigm is based on our previous work in which typically functioning adult participants were asked to remember a spatial pattern of five sequentially presented crosses and indicate whether a comparison pattern presented afterwards matched the remembered one (Martin, Houssemand, Schiltz, Burnod, & Alexandre, 2008). We manipulated the same type of grid as used in Martin et al. (2008) in order to create two levels of interference with their corresponding two levels of executive interference control. We hypothesized that DD children would rely more strongly on frontal resources when the visual aid of the grid was not present

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III.1

Differential Network Activation in Children with Developmental Dyscalculia

Dennis Croonenberg[1,2], Romain Martin[1], Alexander Sack[2], Christine Schiltz[1]

1 Université du Luxembourg, Faculty of Language and Literature, Humanities, Arts and Education, ECCS, Esch-Sur-Alzette, Luxembourg

2 Maastricht University, Department of Cognitive Neuroscience, Vision and Awareness Lab, Maastricht, The Netherlands

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Abstract

Children with Developmental Dyscalculia (DD) show impaired numerical and spatial abilities, often characterized by a diminished activation in neural networks for calculation and visuo-spatial working memory (VSWM). In the current study we investigated the differences in brain activation between children with DD, control children and adults during a VSWM-task and an addition task. During these tasks, we provided a visual aid in the form of a grid during half of the trials.

By presenting the before mentioned conditions during an event-related fMRI-experiment we found that children with DD were affected differently by the aiding grid than the two control groups, leading to a heightened activation of the anterior cingulate cortex and early visual cortex when the grid was absent. In line with both imaging and behavioural data, the current results point towards a deficit in executive control for children with DD during visuo-spatial tasks indicating that DD might be paired with difficulty in suppressing irrelevant spatial information.

Keywords: Developmental Dyscalculia, fMRI, Visuo-Spatial Working Memory, Arithmetic, executive control, Working Memory, anterior cingulate cortex, early visual cortex

1. Introduction

Developmental Dyscalculia (DD) is a learning disability characterized by a decreased ability to perform mathematical operations combined with an intelligence level which is considered to be normal (Butterworth, 2005a; Gross-Tsur, Manor, & Shalev, 1996; Hitch & McAuley, 1991; Mussolin, Mejias, & Noël, 2010). Even during basic tasks such as number comparison and counting small numbers of dots, dyscalculic individuals persistently show reduced fluency (Butterworth, 2005a; Geary, 1993). Problems with representing and understanding numerosity as well as impairment in acquiring and retrieving arithmetic facts are two tendencies that seem to be at the core of this performance deficit (Butterworth, 2005b).

The difficulties DD children have with retrieving and learning arithmetic facts are frequently also characterised by reduced executive function in relation to working-memory (WM) performance (Hitch & McAuley, 1991; McLean & Hitch, 1999). Working memory is classically divided into phonological loop (when dealing with verbal material), visuo-spatial sketchpad (when dealing with visuo-spatial material) and executive control, all of which have been associated with mathematical operations or strategies (Baddeley, 1992; Baddeley & Hitch, 1974). A crucial fourth component has been added to this model by Baddeley (2000) named the episodic buffer. This component comprises a limited capacity system that provides temporary storage of information in a way that it can bind information from multiple systems such as long-term memory and the other WM-systems, and represent this information episodically (Baddeley, 2000). Although it has been argued that this system might be important for the performance of complex arithmetic, no empirical evidence has been supplied for this statement as of yet.

A reliable working memory is of high importance to optimal mathematical functioning as it serves to maintain an active representation of external stimuli, procedures and internally generated elements while solving mathematical problems. Not surprisingly, children with higher mathematical proficiency levels tend to have larger WM capacities (Geary et al., 2007); for review see: LeFevre, DeStefano, Coleman, and Shanahan (2005). Geary's (1990) hypothesis concerning the origins of mathematical difficulties attributes a crucial role to WM functioning in relation to typical and atypical arithmetic facts learning. It postulates that a math-related connection cannot be made at a neural level if the working memory does not keep both the problem and its solution active simultaneously. This view also implies that impairments in working-memory cause an inability to resort to strategies requiring a higher cognitive load (i.e. higher load for working-memory), resulting in a necessity to fall back on simple techniques such as finger counting (Geary, 1990, 1993; Geary & Hoard, 2005; Price, 2008). When testing simple arithmetic performance, children with DD thus tend to demonstrate lower performance and speed in single-digit addition and subtraction. They do, however, seem to have the most notable impairments when handling division and multiplication, which are thought to be due to either a lack of reliable fact-retrieval or due their higher need for multiple operations and carry-procedures (Kaufmann, 2008; Landerl, Bevan, & Butterworth, 2004).

Based on these and other behavioural deficiencies Wilson & Dehaene (2007) propose three subtypes of DD. The first is based on a deficiency in the processing or representation of numerosity (the number sense subtype) and is proposed to be due to a deficiency in the intra-parietal sulcus (IPS). The second subtype is described as a deficiency in spatial attention or executive control, causing participants with DD do perform worse on tasks that require participants to locate a number on a number line, perceive the order of stimuli and written calculations. This subtype is argued to be due to a deficiency in the posterior superior parietal lobule (PSPL). Finally, Wilson & Dehaene (2007) describe the third subtype as being linked to the angular gyrus and perisylvian areas and accounting for verbal difficulty (such as fact retrieval) that children with DD possess.

Rubinstein and Henik (2008) try to account for behavioural deficits in DD and math-learning deficiency as well as deficits seen due to comorbidity with ADHD and dyslexia, by proposing three frameworks based on neural deficits in IPS, Angular Gyrus and frontal regions. The first framework proposes a deficit in IPS as solely being causally responsible for behavioural deficits in DD, specifically in processing numerical quantities. This is backed up by empirical studies that have found lower proficiency in representing either symbolic (Rousselle & Noel, 2007) or non-symbolic (Price, Holloway, Räsanen, Vesterinen & Ansari, 2007) quantities in DD children. Furthermore, imaging studies have found that the representations of numerosity consistently show the IPS as a locus of activation in typical participants (Kanjila, Lane, Feigenson & Bedny, 2015; Bulthé, de Smedt, Op de Beeck, 2015;

Chick, 2014, Harvey, Fracasso, Petridou & Dumoulin, 2015; Piazza, Izard, Pinel, Le Bihan & Dehaene, 2004).

However, since most cases of DD involve multiple deficits, Rubinstein & Henik (2008) propose a second alternative framework in which they argue that attention and working-memory are affected in MLD and DD due to deficiencies in IPS, frontal brain areas and/or fusiform gyrus. They also argue that several additional cognitive functions are involved in numerical calculation which are either related to linguistic representation, exact calculation or the retrieval of arithmetic facts and are represented by different neural networks. However, they do not give a single solution for what might be the direct causal relation between the brain areas and specific deficits and even argue that a deficiency in a single region might cause multiple problems.

The third framework concerns the interpretation of multiple behavioural disorders, arguing that a single deficit in IPS or angular gyrus might cause co-morbitiy of DD with ADHD or dyslexia (Rubinstein & Henik, 2008; Rubinstein, 2015).

Given the involvement of IPS in spatial processing and the claim that a deficit in IPS might be at the heart of DD it becomes important to describe some neuronal characteristics which are associated to visuo-spatial WM (VSWM) functioning in DD-subjects. It has been argued that VSWM-deficiencies are a source of vulnerability in children who have trouble with acquiring mathematical skills (Menon, 2016). For instance, when compared to age-matched controls, children with DD have a relatively smaller grey matter volume in frontal and parietal regions (Rotzer et al., 2008) that are known to underlie VSWM in adults and children (Ashkenazi, Rosenberg-Lee, Metcalfe, Swigart, & Menon, 2013). Similar observations were made using an adaptation of the Corsi block-tapping task (Rotzer et al., 2009). In this experiment, participants had to indicate whether a red circle appearing in a 4x4 grid was situated at the same location as a previously presented circle. Again, children with DD revealed less pronounced activation in the intraparietal sulcus, middle occipital gyrus and inferior frontal gyrus than age-matched controls. The areas which showed diminished activation were part of a fronto-parietal network for arithmetic and mathematics known play an important role in the development of mathematical skills (Rotzer et al., 2009). Diminished neural activity of fronto-parietal networks could also be observed directly when children with DD perform numerical tasks. The intra-parietal sulcus inferior frontal gyrus and anterior cingulate gyrus all revealed a significant rise in activation during approximate and exact calculation for typical children. Although DD subjects displayed activation of the same cortical areas, they did so to a much lesser extent. This indicates that they were not making as much use of the resources dedicated to the processing of number magnitudes as typical children (Kucian et al., 2006) A longitudinal fMRI study by (Dumontheil & Klingberg, 2012) provides further critical evidence for the causal role that intra-parietal sulcus neurons play in both VSWM and numerical operations. These authors reported that brain activity in the intra-parietal sulcus during a VSWM-task in six-to-sixteen year-old participants was indeed predictive of participants' mathematical performance two years after scanning, over and above their performance in behavioural tests.

Considering that mathematical and VSWM processes show a large overlap in cortical sites and have systematically been associated with DD, it becomes imperative to further investigate how they interact with related cognitive processes associated with frontal resources such as executive control. In a study by Supekar & Menon (2012) it was found that children who portrayed weaker regulatory influences from frontal regions over the parietal cortex achieved lower performance in math tasks. Furthermore, in another study children (aged 9) with DD portrayed both impaired VSWM capabilities as well as impaired attentional inhibition function (Szucs, Devine, Soltesz, Nobes & Gabriel, 2013). An interesting case in this context is M.O., a 14 year-old adolescent with DD whose performance in multiplication- and division-problems showed a much larger impairment than that in addition and subtraction (Kaufmann, 2002). It was argued that these problems reflect an impaired central executive that is particularly noticeable during multiplication and division since these operations imply higher WM-load (Kaufmann, 2002). Another sign of a central executive deficit was the need of M.O. to write down intermediate answers when doing multi-digit operations, reflecting an inability to do mental carry-procedures. De Visscher and Noël (2013) recently supplied an additional case-study where a person with dyscalculia showed a similar central executive impairment. They studied DB (42-43 y. o.) in depth in order to characterise her profile of DD. A major finding of this study was that despite DB's high level of intelligence and normal functioning of attentional and memory-resources, she showed the largest difficulty with multiplication problems where interference due to the content of the problem was the largest (De Visscher, Berens, Keidel, Noël, & Bird, 2015). Control of interference is an important function of attention in general that is largely attributed to CE-proficiency (Anderson, 2003; Logan & Gordon, 2001; Rubinstein, Meyer, & Evans, 2001; Szmalec, Vandierendonck, & Kemps, 2005).

The present study aims to better understand how mathematical proficiency relates to visuo-spatial working memory and executive control processes. Concretely, we investigated how adults as well as children with and without specific learning difficulties in mathematics deploy executive control processes in the context of a VSWM task. The experimental paradigm is based on our previous work in which typically functioning adult participants were asked to remember a spatial pattern of five sequentially presented crosses and indicate whether a comparison pattern presented afterwards matched the remembered one (Martin, Houssemand, Schiltz, Burnod, & Alexandre, 2008). This test is similar to the Corsi-blocks task, where participants have to point at a multitude of blocks in the same order as previously done by the experimenter (Vandierendonck, Kemps, Fastame, Szmalec, & Arnaud, 2004). This task is reflective of working-memory capacity and also requires participants to remember spatial locations. We manipulated the same type of grid as used in Martin et al. (2008) in order to create two levels of interference with their corresponding two levels of executive interference control. In the original study, the presence/absence of a grid explicitly delimiting the sixteen possible locations of the cross appearances modulated the executive load of the visuo-spatial task, as well as the associated activation levels of the parietal cortex, the cuneus, the lateral prefrontal cortex and the anterior cingulate cortex in typical adult participants. The current study was set up to expand these results and investigate whether the areas that are involved in handling this type of VSWM tasks react differently for children with DD than for typically developing children or adults. Integrating an aiding spatial structure (i.e. grid) into a VSWM task thus allowed us to explore the activation characteristics of DD in relation to visuo-spatial working memory while putting an emphasis on the role of executive control.

Using this original VSWM design we compared children with DD to age-matched typically developing children in order to highlight what differentiates them from typical development. Furthermore, both typical children and DD children were compared to an adult group that was assumed to be highly proficient at the tested tasks. It was expected that adults would possess a fronto-parietal network that was more attuned to the task, whereas the control children would still show signs of development such as increased recruitment of frontal resources. Thus, the adult group functioned as a comparison to further investigate developmental aspects related to the task as typically developing children could be compared to a typical adult population.

To reveal the functional overlap between visuo-spatial working memory and mathematical operations, we implemented a VSWM and an addition (ADD) task. Both tasks contained the same types of spatial stimuli, but differed in their instruction. The participants were either instructed to remember locations (VSWM) or to add the amount (ADD) of stimuli. An important feature of the current design is that for both tasks only small quantities of stimuli were used. This was done to ensure that control and DD children would show an acceptable level of proficiency. This way, it was possible to focus on representations of small quantities and how they are handled differently for spatial or numerical purposes. Furthermore, the grid manipulation deployed for the VSWM task was also used in the addition task to allow for a better comparison as it was not expected to interact with this task. To control for generic perceptual effects both VSWM and ADD conditions were juxtaposed with passive equivalents (PAS), yielding a third condition which served as a baseline during the experiment. We expected the grid to cause an alleviation of frontal resources in the VSWM but not in the ADD task, resulting in a lower activation of these regions, with the DD children benefiting from the grid to a larger extend than the control children and the adults.

Methods

Participants

10 children with DD (5 girls and 5 boys, mean age 11.1+/-1.6 years) participated in the experiment. All of them were selected from participation in a prior fMRI study by Mussolin, De Volder, et al.(2010). Another 10 children (5 girls and 5 boys, mean age 11.3 +/- 1.2 years) as well as 10 adults (5 women and 5 men, mean age 25.6 +/- 1.9 years) with no history of learning disabilities served as control groups, resulting in 30 participants in total.

All the children assigned to the DD-group were diagnosed as having developmental dyscalculia by the neuro-pediatric department of the UCL University Hospital St-Luc and had a two-year delay in school performance in mathematics without literacy problems. In addition they achieved atypically low scores on two paper and pencil neuropsychological tests assessing numerical abilities (for further details on these tests see 'Neuropsychological testing').

The legal guardians of the participating children provided written informed consent prior to the experiment. None of the participants suffered from any other neurological, psychiatric or any developmental or learning disorders (e.g. dyslexia) outside of DD. The study was approved by the local ethical committee based on the World Medical Association's Declaration of Helsinki (WMA, 2001). One female participant from the DD-group was excluded from further analysis due to excess motion in the scanner.

Neuropsychological testing

General cognitive abilities were assessed (in French) for both the DD-group and the typically developing children. To calculate an IQ-estimate, children performed the Similarities and Images Completion subtests of the WISC-III (Wechsler, 1996). For both these groups, two measures to assess their reading ability were performed. Firstly, the L3 task (Lobrot, 1980) where children have to silently read a maximum of 36 unfinished sentences. Children have to complete these sentences using one of five available words. The second test involving reading comprised of a list of words in which children were given one minute to read as many words as they can (one-minute reading, Khomsi (1999)).

To assess verbal short-term memory, both groups of children performed a backwards and forward word-span task. Children were presented with a series of words that increased over repetitions. They were asked to repeat them in the presented order (forward span) or reversed order (backward span).

To assess spatial short-term memory, children performed a Corsi block-tapping test. During this task, the children had to point out an increasing number of block positions on a grid according to a pattern that was previously pointed out by an experimenter.

Furthermore, the children were tested concerning their central executive capabilities with regards to working memory. In this test, the children were read a set of sentences and had to indicate whether they were true of false. When the set had ended, the child was asked to name the last word of each sentence.

Finally, children's arithmetic performance was measured using two written tests. First, the Kortrijk Rekenen Test (KRT; Cracco et al. (1995)) which is a normalized test consisting of complex calculations and mathematical problems. The second arithmetic test consisted of timed calculation were the participants had to solve as many simple calculations as they could for each operator (Addition, Subtraction, Division & Multiplication). For this they were given two minutes per operation.

As it was expected that adults were highly proficient at the neuropsychological tests, which would lead to a non-interpretable result, they did not have to perform these test

Stimuli and tasks

The experiment consisted of two main tasks. The *addition-task* (ADD) presented the participant with three consecutive patterns of two or three crosses on a white-noise background in a 4x4 grid. Participants were asked to add the number of crosses mentally. At the end of each trial they were asked if the outcome of the addition matched the value of the digit presented centrally on a grey background. The second task was a *VSWM-task* in which participants had to remember the location of three consecutively presented single crosses in the same 4x4 layout and match it to a final pattern. Both tasks offered either a condition in which there was a grey grid present that separated the 16 potential cross locations or a condition in without grid. All conditions had a *passive equivalent* with identical timing and visual stimulation but no response was required.

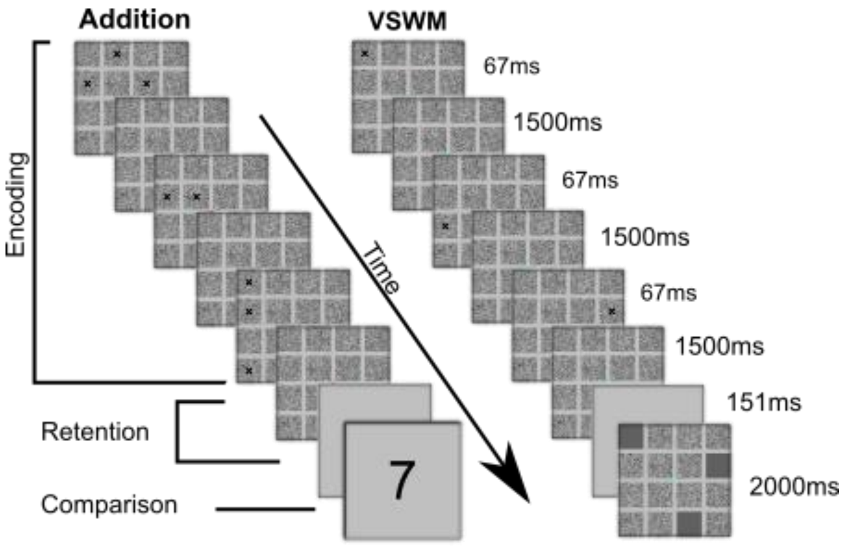

Figure III.1.1. *Timeline of addition and VSWM trials (with grid). Participants were instructed to mentally add the amount of crosses (addition) or remember their locations (VSWM). Both tasks consisted of one condition in which the grid was present (as depicted) and one where it was absent.*

Imaging parameters

Subjects were scanned using a slow event-related design with a 1.5T Philips (Gyroscan Intera) scanner provided with standard quadrature birdcage head coils at the Catholic University of Louvain, St-Luc Clinic. In each session, a 3D T1-weighted data set encompassing the whole brain was acquired for every subject (110 slices, 1.5 mm slice thickness, matrix size = 256x256x256). These anatomical images were used for normalization of the functional images. T2*-weighted multi-slice gradient-echo-planar imaging (EPI) was performed using the blood oxygen level-dependent (BOLD) contrast effect as an indirect marker of local neuronal activity (Ogawa S et al., 1990). In each experiment, thirty-three 3.6 mm axial slices (TR = 3000 ms, TE = 40 ms, FA = 90°, matrix size = 64x64, FOV = 210x210) were acquired. We performed 4 runs lasting 5min 47sec 424ms (116 TRs) and total time in the scanner was about 40 min. The participants' head was restrained by foam pads.

Analysis

Behavioural analyses

Student t-tests were performed for comparing differences in reaction-times and accuracy between groups. For the influence of grid-manipulation during the tasks a repeated-measures GLM was performed, including two within-subject factors for condition (ADD & VSWM) and grid (grid, no-grid) respectively and one between-subject factor for group (Control Children, DD-Children and Adults). To inspect the effects of grid per condition, pair-wise comparisons were made using t-tests.

Pre-processing of imaging data

The fMRI signal in the different conditions was compared using BrainVoyager QX (Version 2.6, Brain Innovation, Maastricht, the Netherlands) by applying a regression analysis. Pre-processing consisted of a linear trend removal for excluding scanner-related signal, temporal high-pass filtering to remove temporal frequencies lower than 3 cycles per run, slice-timing correction and motion correction (rigid body correction, three translations and three rotations). Data were smoothed in the spatial domain (4 mm FWHM) to reduce the residual anatomical and functional variability between participants.

To facilitate comparison of the locations of activated brain region across subjects all anatomical as well as functional volumes were spatially normalized [Talairach-transformation; (Talairach & Tournoux, 1988)] and the statistical maps computed were aligned and overlaid to 3D T1-weighted scans to calculate Talairach coordinates for all relevant activation clusters.

Statistical maps and Regions of Interest

Functional data were analysed using multiple regression models (General Linear Model; GLM) consisting of predictors, which corresponded to the tasks (VSWM & ADD) and grid conditions (grid, no-grid). The predictor time courses used were computed on the basis of a linear model of the relation between neural activity and hemodynamic response, assuming a rectangular neural response during phases of visual stimulation (Boynton, Engel, Glover, & Heeger, 1996).

The contrasts of interest were computed at the individual level to identify the cerebral regions significantly activated by each condition. Significant cerebral activations were then examined at the group level in random-effect ANCOVA analyses, with the statistical threshold set at a False Discovery Rate of 0.01 and extending to at least 20 contiguous voxels.

To further investigate potential group differences in brain activation for the working memory and addition tasks, regions of interest (ROIs) were extracted. ROIs were defined by overlaying the activations with standardized maps and manually selecting foci in activated clusters for the random effect analysis of the adult control-group for VSWM (vs. PAS) at an FDR corrected level of $p < 0.01$. In order to investigate potential effects of executive control mechanisms, ACC was selected as an additional ROI based on the same VSWM (vs. PAS) maps in DD-subjects.

Since the VSWM-task elicited a large uninterrupted activation, it was split into subcomponents based on anatomical location (see table 6). Significantly activated voxels were selected within a maximum cubic range of 20 pixels for subsequent comparisons.

The subdivision of the uninterrupted activation resulted in bilateral clusters of activation around the Occipital lobe in early visual cortex (EVC) (that included medial parts of the calcarine sulcus leading up to the occipital-sulcus), Occipito-Parietal junction, Posterior Intra-Parietal Sulcus (P-IPS), Anterior IPS A-IPS and Superior Frontal Gyrus (SFG). Three areas were selected for further analysis based on the representative characteristics of their event-related activation patterns.

For each subject, the average event-related BOLD-signal for each ROI at the peaks (3 and 4 TRs after onset of the first cross) was extracted to make comparisons between grid and no-grid conditions. Consequently, a repeated measures GLM was performed in order to distinguish between the influences that grid manipulation had in different groups and tasks.

Results

Neuropsychological Tests

	Control children	DD children	*t*
Descriptive information			
N	10	9	
Gender (M/F)	5/5	5/4	
Age (months)	128.9 (13.0)	123.4(18.4)	0.96
IQ			
Similarities (raw scores)	14.8 (2.2)	12.6 (2.1)	2.12
Images completion (raw scores)	11.6 (3.0)	11.4 (2.2)	0.14
IQ estimated	118.3 (12.6)	111.6 (10.4)	1.24
Mathematics			
KRT score	15.4 (5.5)	5.3 (3.5)	4.57**
One-minute addition	23.6 (7.4)	13.9(7.5)	2.68*
One -minute subtraction	18.3 (6.0)	11.2(7.0)	2.20*
One -minute multiplication	15.3 (5.5)	9.4(5.3)	2.20*
Reading			
L3 (correct sentences)	30.0 (4.5)	22.6(7.1)	2.54*
One-minute reading (correct words)	72.1 (7.7)	63.8(4.2)	1.74
Working memory			
Forward span words	4.0 (0.8)	3.9(0.3)	0.40
Backward span words	3.3 (0.5)	2.8(0.3)	2.33*
Corsi blocks span	5.5 (1.0)	5.0(1.1)	0.94
Listening span	3.6 (1.1)	3.0(0.8)	1.71

Table III.1.1. *Results from pre-experimental neuropsychological tests. Please note that standard deviations are shown in parentheses.* * $p < 0.05$, ** $p < 0.01$

The cluster of mathematical tests was the main source of difference between the two groups, systematically yielding a weaker performance in the four math tasks in DD compared to control children. DD-children also read less sentences correctly (L3) and achieve a lower backwards word-span than the control children of the present study, which might be due to a comorbidity with dyslexia (Von Aster & Shalev, 2007). For the visuo-spatial working-memory tasks DD-children performed at a comparable level to that of the control children. Since participants do not seem to differ on our measures of general intelligence, they make for a perfect comparison to the control children because the main source of their neurological differences stems from their lowered ability to perform mathematical operations.

Behavioural results

Accuracy

In the VSWM task accuracy was high, for adults (95%, SD 6.26%), for typical children (83.7% SD 14.32%) and for children with dyscalculia (72.9%, SD 24.66%). In the addition task adults answered correctly in 99% (SD=2.38%) of the trials and control-children and DD-subjects had an accuracy of 92.8% (SD=7.4%) and 95.0% (SD= 5.15%) respectively. Multiple comparisons revealed adults to be significantly more accurate than DD-children in both the addition ($p=0.002$) and VSWM task ($p<0.001$). The difference between children and adults was not significant in both tasks ($p=0.153$ for addition and $p=0.066$ for VSWM). For all groups, accuracy was significantly lower in the VSWM task (Adults: $t=3.277$, $P=0.004$; Control Children: $t=2.766$, $p=0.012$; DD-Children 3.347; $p=0.009$). The VSWM task revealed a significant aiding effect of grid-manipulation only for typically developing children ($F(2,27)=9.8517$, $p=0.013$) but not for adults($F(2,27)=0.647$, $p=0.442$) or DD-children ($F(2,27)=1.967$, $p=0.198$). The addition task portrayed no significant effects of grid for any of the three groups. For details, see supplementary material.

Reaction times

With the exception of one participant in the group of control-children, all subjects revealed a higher average reaction time in the VSWM task than the addition-task.

Differences between the ADD and VSWM task were on average 272ms (SD=86.3, t(2)=90.8, p <0.001) for adults, 251ms (SD= 132,6, t(2)=31.9, p <0.001) for typically developing children and 273ms (SD=165.90, t(2)=26.0, p=0.001) for children with DD respectively. A second observation is that during the working memory task, adults reacted significantly faster than typical children (t(17)=-4.614, p<0.001) and children with dyscalculia (t(17)=-3.792, p=0.001). Although typically developing children on average reacted faster than DD-children, this difference was not significant (t(17)=-1.211, p= 0.242). In the addition task, a similar pattern could be observed. Adults were faster than both typical children (t(17)=-4.415, p<0.001) and children with dyscalculia (t(17)=-5.919, p<0.001). Again, the reaction time comparison between children with DD and typical Children revealed no significant difference (t(17) = -1.291, p= 0.21).

Manipulation of the grid revealed a trend towards longer reaction times in the VSWM-task for the no-grid condition in both control children (F(2,27)=4.563, p=0.061) and DD-children (F(2,27)=4.581, p=0.065). The addition-task portrayed no significant influence of the grid for all of the groups Adults (F(2,27)=0.019, p=0.894), Control-children (F(2,27)=0.028, p=0.872), DD-Children (F(2,27)=0.897, p=0.371)).

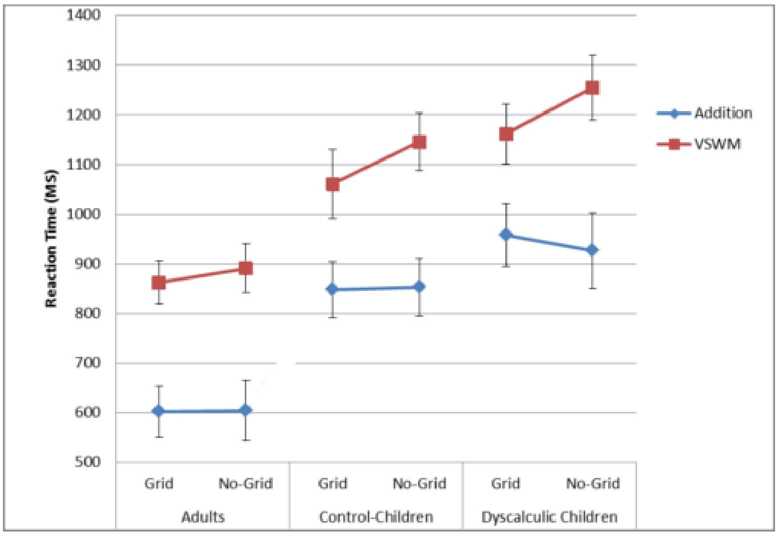

Figure III.1.2. *Reaction-times for addition and VSWM-Task.* In both tasks adults were significantly faster than both the control and DD-children, whereas the control and DD-children did not differ significantly. All groups portrayed faster reaction times during the ADD-Task suggesting that the VSWM-task was harder.

Imaging results

Visuo-spatial working memory and addition networks

	EVC		OP		A-IPS		ACC	
	f	**p**	**f**	**P**	**f**	**p**	**f**	**p**
Adults	-6.825	<0.001**	-6.838	<0.001**	-3.284	0.004**	0.019	0.985
Control-children	-5.021	<0.001**	-8.414	<0.001**	-3.446	0.003**	-1.569	0.134
DD-children	-5.622	<0.001**	-8.499	<0.001**	-3.425	0.003**	-1.062	0.304

Table III.1.2. Condition-effects on BOLD event-related averages (VSWM > Addition) for the four ROI's that were selected for further analyses; Early Visual Cortex (EVC), Occipito-parietal cortex (OP), the anterior intraparietal sulcus (A-IPS) and Anterior Cingulate Cortex (ACC). Of these four areas, all showed a significantly higher BOLD-response during VSWM task, with exception of the ACC.

By contrasting the VSWM-task and its passive equivalent (VSWM>Passive), activation related to visuo-spatial working memory was brought to light. In the three groups, posterior parts of the brain showed large areas of activation extending from the early visual cortex (EVC) up to the anterior parts of the IPS (A-IPS) in a large uninterrupted activation including the occipito-parietal (OP) cortex and posterior IPS (P-IPS). Further preferences for the VSWM-task were observed in the Superior Frontal Gyrus and Supplementary Motor Area. Particularly interesting is that adults portrayed the largest spatially uninterrupted activation of the three groups, followed by the control-children who seem to recruit the same resources, but to a lesser extent. Averaged t-values were even lower and significantly activated regions comprised even fewer voxels for the DD-group (See supplementary tables 5 & 6). The same tendency could be seen in the (ADD>PAS) contrast. Adults showed a large activation that was more dispersed in control-children and almost disappeared in participants with DD (table 7). Similarly all t-values descended when contrasting groups, where those of adults were higher than those of typical children and finally DD-children. As shown in figure III.1.2 the ADD-task also caused an increase in BOLD-signal that largely overlapped with the activation found in the VSWM-task. Three of the four anatomical regions (i.e. EVC, OP and A-IPS) that were selected for further comparisons revealed a significantly higher activation during the VSWM-task (VSWM>ADD). In contrast, the ACC did not yield a difference between the conditions for all three groups.

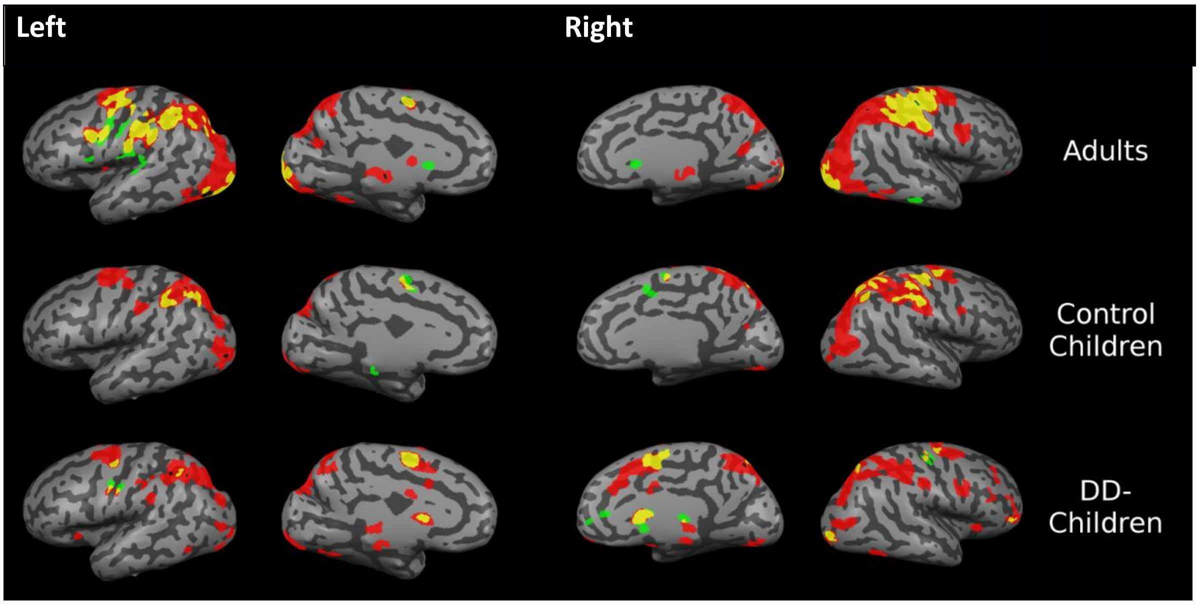

Figure III.1.2. *Contrast for VSWM-task > Passive (Red), ADD > Passive (Green) and their overlap (Yellow) at a threshold where FDR=0.01. The activation for the ADD-task largely overlapped the activation for the VSWM-task. Activation of the ACC was only found for DD-participants in the VSWM-task.*

Effect of the grid:

When contrasting event-related averages for the two grid-conditions in the VSWM-task an effect was found in two areas (see table 8). First and foremost the early visual cortex, where the presence of a grid induced a significantly higher activation for both the adults and control-children, but this activation was absent for dyscalculic children. Although part of the activation increase in the two control groups can be attributed to mere visual stimulation, the lack of a similar increase in the DD subjects potentially also signifies a deficit in facilitating the perceptual processes required for this task.

The second area that exposed a clear influence of the grid during the VSWM-task was the ACC. The absence of a grid caused an increase in activation only for dyscalculics but not for the control subjects. We propose that this recruitment of the ACC in the no-grid condition indicates the DD subject's increased need of executive control resources when a spatial structure is absent during the visuo-spatial working-memory task.

For the occipito-parietal cortex, anterior & posterior IPS, SFG and SMA, no clear differences between the two grid-conditions were found for the three groups.

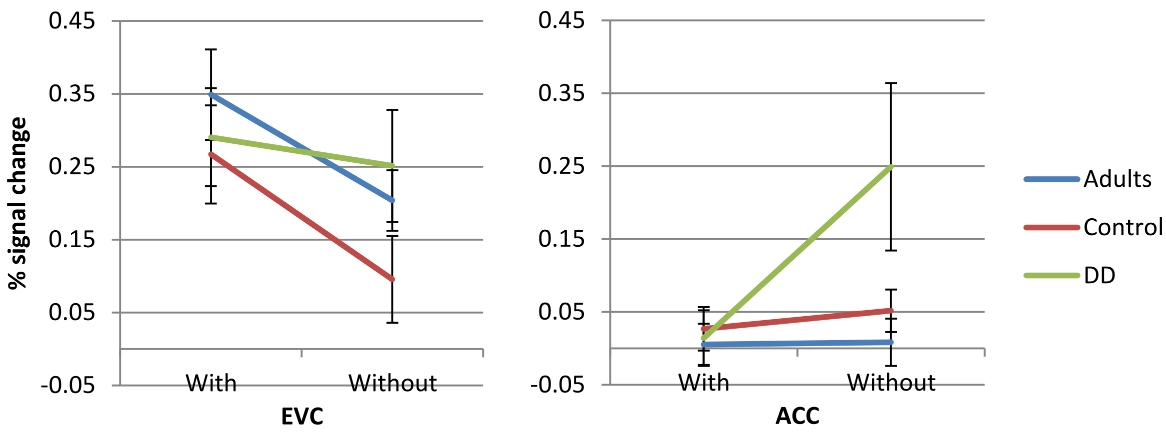

Figure III.1.3: *Changes in BOLD-amplitude (%) for peak-activations of the EVC (left) and ACC (right) in the VSWM task for both the grid and no-grid conditions. Both areas revealed a significant group*grid interaction.*

	EVC		OP		A-IPS		ACC	
	f	**p**	**f**	**p**	**f**	**p**	**f**	**p**
Main Grid-effect	1.44	0.275	0.107	0.746	0.84	0.685	7.342	**0.012***
Grid * Group	4.523	**0.02***	0.492	0.617	0.08	0.923	6.788	**0.029***
Grid-effect Adults	11.06	**0.009***	1.233	0.297	0.176	0.685	0.024	0.880
Grid-effect Control Children	25.5	**0.001***	0.709	0.422	1.235	0.295	0.790	0.397
Grid-Effect DD Children	2.087	0.182	0.24	0.636	0.213	0.656	6.433	**0.035***

Table III.1.3. *Result of repeated measures analysis of the event-related peak-activations in the VSWM-task for four of the selected ROI's* (Bonferroni-corrected *(4)). A clear difference between grid and no-grid conditions, corresponding to a higher activation in the grid-condition, was present in both control groups in the EVC, but not dyscalculics.. Contrastingly, exclusively the dyscalculic children exposed higher activation in the ACC in the grid-condition.*

	EVC		OP		A-IPS		ACC	
	f	**p**	**p**	**p**	**f**	**p**	**f**	
Main Grid-effect	2.04	0.18	3.66	0.07	0.19	0.86	0.13	0.91
Grid-effect * Group	0.19	0.87	0.11	0.92	0.45	0.70	1.62	0.25
Grid-effect (Adults)	0.64	0.59	0.14	0.90	0.71	0.55	1.64	0.24
Grid-effect (Control Children)	4.81	**0.04***	3.24	0.08	0.55	0.64	2.47	0.13
Grid-Effect (DD children)	0.10	0.93	0.62	0.60	0.08	0.94	0.83	0.49

Table III.1.4. *Result of repeated measures analysis of event-related peak-activations in the ADD-task for four of the selected ROI's (*Bonferroni-corrected *(4)). Opposed to the VSWM-task, averaged peak-activations neither differed significantly between the grid-conditions in the early visual cortex (EVC) nor the anterior cingulate region (ACC).*

Discussion

The current study was set up to investigate how mathematical proficiency is related to visuo-spatial working memory and executive control processes in typical and atypical mathematical development and what the neural correlates of this relation are. Concretely, we assessed whether children with DD are influenced differently than typically developing children and adults by the presence of an aiding visual grid surrounding potential target-locations during a VSWM-task. Due to the structuring nature of the grid that is dividing the problem-space into discrete regions of possible locations, we hypothesized that its presence would facilitate performance by reducing the amount of potentially wrong locations . In order to control for the effects of low-level visual stimulation induced by the grid, we presented the same grid in an ADD-task where spatial location of the stimuli was irrelevant to the task. When contrasting both VSWM and ADD task conditions with their passive counterpart, we observed activations throughout a fronto-parietal network that were less pronounced for DD children than control children and adults. Furthermore the presence or absence of a grid during the VSWM task affected DD children differently than both control groups. In accordance with our hypothesis that DD children would rely more strongly on frontal resources when the visual aid of the grid was not present, DD children showed significantly higher ACC activation than both control groups in the no-grid condition. At the same time, the grid presence/absence did not significantly affect BOLD responses of adults and control children in this frontal region. Conversely, removing the grid significantly decreased activation in early visual cortex for both control groups, but not for the DD children. The impact of this result was reinforced by the fact that the difference on neuropsychological tests was minimal between typical children and DD children with regards to intelligence and linguistic measures. Furthermore a lack of a difference in task performance-accuracy during the scanning comes from the fact that the task was relatively easy, therewith preventing our results to be confounded by higher error-rates for DD-children. It is therefore highly unlikely that the current results stem from a difference in general intelligence or generic cognitive abilities between the groups of children.

An inability to suppress incorrect locations or answers could explain why children with DD portray (a) a relatively high level of activation in EVC (compared to the two other groups and compared to their own activity level in the no-grid condition), as well as (b) a heightened ACC activation during the more difficult no-grid task. We propose that this relation between abnormal activation levels in the EVC and the recruitment of the ACC signifies an increased need for executive interference control in dyscalculic participants. In accordance with the account of De Visscher and Noël (2013), DD children might be abnormally susceptible to interference caused by non-target locations and controlling this interference requires employment of the ACC. Furthermore, incorrect potential locations might not be suppressed as efficiently as in the control groups, explaining the heightened activation of the EVC in the DD group.

The ACC is known to play an important role in executive control and it is observed in a variety of studies due to its role in monitoring response conflict (van Veen, Cohen, Botvinick, Stenger, & Carter, 2001). It has thus been associated with a wide array of tasks, ranging from emotional processing to oculomotor-planning and speech (Bush, Luu, & Posner, 2000; Offringa et al., 2013; Paus, Petrides, Evans, & Meyer, 1993). Whenever there is an extra need for adjustments in behaviour or monitoring performance, ACC involvement can be found (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Hirsh & Inzlicht, 2010; Van Veen & Carter, 2002). With respect to mathematical tasks higher ACC activation was reported during approximate calculation, rather than exact calculation which is proposed to reflect higher attention and working memory loads during approximation (Kucian et al., 2006). ACC activation is also frequently seen during incongruent trials in Stroop tasks (Roelofs, Van Turennout, & Coles, 2006; Ruff, Woodward, Laurens, & Liddle, 2001; van Veen et al., 2001; Zysset, Müller, Lohmann, & von Cramon, 2001)

While Censabella and Noël (2007) did not find any evidence for lowered executive function when assessing performance in Stroop and flanker tasks in children with mathematical difficulties, Askenazi and Henik (2010) propose that persons with DD could have difficulties in inhibiting irrelevant responses or monitoring response conflict when presented with a numerical Stroop task. DD participants also showed an effect of interference (incongruent minus neutral) when an attentional load was added to the numerical Stroop task in contrast to typically developing adults (Askenazi & Henik, 2010). Furthermore, significant activity in the ACC was present during this same task in healthy young adults when incongruent trials were compared to conflict-free congruent trials (Kaufmann et al., 2005).

The significant increase of ACC activation observed in the DD children of the present study can be interpreted as an indicator of increased difficulty in the VSWM task without grid. People who are proficient at the VSWM task are assumed to have a more precise and accurate positional representation of the stimuli present in working memory. Consequently the extra ACC activation in dyscalculia might be a result of interference of irrelevant visual information (i.e. positions) which tends to hamper behavioural performance - although in the present case DDs were not significantly less accurate or faster than the typical children. This lack of a statistically significance difference was probably due to the fact that we deliberately chose an easy version of the VSWM (which required the encoding and recall of only three positions) in order to avoid confounding behavioural and neuro-functional changes. This inability of the dyscalculics to suppress interference of stimuli might also make it harder to decide whether the reference pattern matches the location of the previously presented stimuli.

An alternative explanation that could account for the respective activation pattern observed in EVC and ACC cortices of DD children might be that they are reflecting the specific need of DD children to mentally represent the grid and therewith make use of their visuo-spatial sketchpad. Effects on the early visual cortex due to a VSWM task are not uncommon. For instance, a contra-lateral activation of the visual cortex is apparent when a stimulus position is held or rehearsed in working memory (Awh & Jonides, 2001). Furthermore, it was also possible to differentiate which of two gratings was held in working memory by looking at the activation pattern in EVC (Harrison & Tong, 2009). Similarly, Martin et al. (2008) found an interaction between the type of required encoding (categorical/coordinate) and a hemispheric activation in the visual cortex. Observing a heightened activation of the ACC fits in this context too, as imagining a grid also requires participants to maintain the grid representation and this type of maintenance is known to induce ACC activation in VSWM tasks (Courtney, Ungerleider, Keil, & Haxby, 1996; Ricciardi et al., 2006; Smith, Jonides, & Koeppe, 1996).

Accounting for the current results by arguing in terms of either (a) control of interference or (b) mental imagery requires the assumption that the heightened activation in the EVC during the 'no-grid' condition is what sets the children with DD apart from the other two groups. However, the opposite might be true. When a grid was present, typically developing children and adults revealed a stronger BOLD-response in the early visual cortex than when the grid was absent. The DD-group, however, showed similar levels of activation during the VSWM-task between the two grid conditions. Considering that in the ADD-condition the BOLD-response to the grid hardly differed between groups, it is unlikely that the functional differences evoked by the grid presence (or absence) in the VSWM task are purely due to differences in visual processing of the grid. When considered from this point of view, it is also possible that the abnormal activation pattern in the DD children's EVS reflects their difficulties in allocating attentional resources to the grid and use appropriately it as a visual aid to structure space and the corresponding encoding locations. Visuo-spatial attention orienting indeed enhances neural processing in visual cortex (Moran & Desimone,1985; McAdams & Maunsell, 1999). It could thus be demonstrated that voluntary attention orienting towards visual stimuli entails multiple foci of cortical enhancement in the corresponding representation zones of the occipital visual cortex (Brefczynski and DeYoe, 1999).

Literature shows that deficiencies in visual processing along the dorsal route (Goodale & Milner, 1992) go hand in hand with decreased mathematical ability. Sigmundsson, Anholt, and Talcott (2010) thus demonstrated that mathematical proficiency is associated with the detection of coherent motion. They found that people who were categorised as poor math achievers also portrayed a lowered sensitivity to the detection of coherent motion. Furthermore, Boets, De Smedt, and Ghesquiere (2011) showed that sensitivity to motion-coherence was predictive of proficiency in subtraction operations as assessed at an individual level three years later. When testing auditory and visuo-spatial interference in mathematical tasks by adding either recorded speech or visual noise to a computerized arithmetic task it was reported that younger children aged about 7 seem to have relatively larger visuo-spatial interference effects. In contrast, the performance of somewhat older children around 9 years of age was hampered more by linguistic interference effects (McKenzie, Bull, & Gray, 2003). This seems to reflect a preference for linguistic strategies at later stages in development as the children are more prone to be bothered by linguistic interference. Given these results, the activation differences in the visual cortex that we found in the current study might be the result of a deficit in perceptual processing and/or learning taking place early in development and lasting into late childhood for DD children. If a child fails to build up processing resources that can tune the visual system to specific tasks, her VSWM functioning might be at risk and all related cognitive functions (such as numerical skills) might be jeopardized indirectly.

In the current VSWM task, DD children were required to keep specific locations in working-memory and they had to incorporate a spatial structure during the “grid-condition”. An appropriately tuned VSWM should allow to both (a) direct attention towards the structuring grid in order to incorporate this helpful information into a memory trace, while at the same time (b) suppressing interference from the locations within the grid that do not contain any cross. For DD children, however, it seems that these modulating systems involved with the visuo-spatial task are less effective, leaving their mark on the neuronal activity levels in the EVC. The lack of this perceptual tuning in children with DD, as seen in the current experiment, could explain a diminished VSWM efficiency causing both a diminished reliability of working-memory traces and their associated long-term representations and an additional need for executive control.

Von Aster and Shalev (2007) argue in their 4-stage model of mathematical development that numeracy acquisition is coupled with a continuous rise in working memory resources during each of the four stages of development. According to them, mathematical development begins with a basic grasp of number sense (cardinality) and via the acquisition of linguistic and symbolic number representations is then resulting in the build-up of visuo-spatial numerical tools. Leibovich and Henik (2013) add to this model by arguing that there are several important steps in perceptual learning that are necessary to establish the cardinal stage as described by von Aster and Shalev (2007). The combination of these two models is currently the only explanation that attempts to describe the development of numerical skills in discrete stages with relation to dyscalculia and makes an argument for a continuous growth of working-memory ability. Given the current results it is possible that the spatial components that are associated with mathematical tasks in early development are a tool for learning both procedural operations and arithmetic fact.

Studying the deployment of executive control in VSWM tasks offers the possibility to learn more about the neural correlates associated with handling different cognitive loads in typical and atypical cognitive development. Particularly interesting is the question how cortical resources are balanced under increasing working-memory loads. For example, contrary to (Klingberg, Forssberg, & Westerberg, 2002) but similarly to (Rotzer et al., 2009) the current study was unable to find activations in the superior frontal sulcus during the VSWM task. This region was found to exhibit sustained activity during the delay period when visuo-spatial information is held in working memory. This result discrepancy may come from differences in task difficulty. Klingberg and colleagues (2002) used both low and high load conditions containing three or five dots that had to be held in WM. In contrast, we only used three stimulus elements that participants had to keep in their working memory, such that the task was simple enough for dyscalculics to perform at a comparable level than control children. The fact that the task was relatively easy also accounts for the lack of behavioural differences between control-children and DD-children during scanning. Future studies should focus on finding the point where children with DD utilize cortical resources to their full extent and the cognitive strategies and neuronal correlates that are involved in coping with this supreme challenge.

The fact that both the EVC and ACC in children with DD respond differently to the presence or absence of a grid in the VSWM task leads us to conclude that they process this type of visual aid differently than typically developing children or adults. We consider that an altered and/or inefficient control of interference of incorrect locations in the without-grid condition is the most likely explanation for our results, since this account could explain both the higher EVC and ACC activations. However, it remains to be determined if the neuro-functional differences which characterize processing of the grid in the DD group are better explained by a perceptual or an attentional deficit. To sum up, we conclude that the current results point towards an altered VSWM functioning in DD that is tentatively countered by recruitment of compensatory frontal resources. If such a deficit model could be confirmed it would offer a new angle of attack with regards to developing coping mechanisms or training interventions for these particular types of processing in dyscalculia.

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Supplementary Material

Accuracy

		Addition		VSWM	
		Average %Correct	**St. Dev**	**Average %Correct**	**St. Dev**
Adults	**Grid**	100	0	96,3	4,9
	No-Grid	98	3	93,6	7,1
Control Children	**Grid**	92,2	7,1	92,2	7,1
	No-Grid	93,5	7,8	75,3	14,7
DD-Children	**Grid**	94,7	4,4	77,1	29
	No-Grid	95,3	5,8	64,3	17,8

Table 1. *Averaged accuracy for both tasks under grid and no-grid conditions.*

	Addition		VSWM	
	F	**P**	**F**	**P**
Overall effect of Grid	<0.001	0.994	9.019	0.006**
Grid * Group	0.485	0.621	1.412	0.262
Grid-effect Adults	3.857	0.081	0.647	0.442
Grid-effect Control Children	0.160	0.699	9.517	0.013*
Grid-effect DD-Children	0.053	0.824	1.967	0.198

Table SIII.1.2. Grid-effects on accuracy revealed that control-children portray an effect of grid during the VSWM-task that seems to be driving a significant main effect.

Reaction times

	Grid	Addition		VSWM	
		Average	Std. Dev.	Average	Std. Dev.
Adults	**Grid**	602,8	239,6	862,6	283
	No-Grid	604,9	268	890,9	330,2
Control-Children	**Grid**	848,3	379,7	1060,2	309,4
	No-Grid	853,3	319,8	1145,4	320,7
Dyscalculic Children	**Grid**	955,5	335,8	1160,3	350,1
	No-Grid	929,8	369,2	1261	421,9

Table SIII.1.3. *Averaged reaction time for all groups during both the VSWM and ADD-tasks containing either a grid or no-grid.*

	Addition		VSWM	
	F	P	F	P
Overall effect of Grid	0.232	0.634	10.466	0.003**
Grid * Group	0.506	0.609	0.958	0.397
Grid-effect Adults	0.019	0.894	1.152	0.311
Grid-effect Control Children	0.028	0.872	4.563	0.061
Grid-effect DD-Children	0.897	0.371	4.581	0.065

Table SIII.1.4. *Effect of grid on reaction-time. A main effect of grid on reaction-time could be seen in the VSWM-task, which did not occur on a group-level.*

Voxel-overlap tables

ROI		Talairach Coordinates			Adults			Control Children			DD-Children		
		X	Y	Z	t	voxels	overlap	t	voxels	overlap	t	voxels	overlap
Left	EVC	-18	-97	-3	6,80	24974	0.45	5,48	9972	0.00	5,18	11952	0.33
Right	EVC	21	-95	-3	6,64	23982	0.42	5,86	18764	0.97	5,00	9052	0.32
Left	OP	-28	-74	28	7,37	25312	0.13	5,96	11570	0.13	5,59	12206	0.01
Right	OP	22	-73	27	6,17	34089	X	5,98	14369	0.15	5,56	15003	0.00
Left	P-IPS	-23	-70	56	7,65	28053	0.24	6,20	12499	0.50	5,64	11420	0.52
Right	P-IPS	20	-66	47	7,20	40110	0.01	6,80	20335	0.41	5,67	18104	0.36
Left	A-IPS	-39	-41	41	8,24	23986	0.25	5,58	11792	0.50	5,53	7793	0.79
Right	A-IPS	37	-34	48	7,10	34393	0.44	5,86	20460	0.47	5,24	9011	0.28
Left	SFG	-26	-11	57	6,47	16288	0.04	6,25	8021	0.19	5,56	7480	0.41
Right	SFG	27	-9	55	6,35	20491	0.47	6,20	10872	0.42	4,02	6061	0.19
	SMA	0	-4	48	4,92	5203	0.30	4,41	460	1.0	5,55	5413	0.85
Left	ACC	-13	36	18							4,98	1816	0.32
Right	ACC	12	35	19							0,83	2640	0.12

***Table SIII.1.5**. Extent of significantly activated voxels and averaged t-values during the VSWM-task and the proportion in which it overlapped with the ADD task. With exception of the ACC, T-values and extent of activation descend for typical children and even further for DD-participants when compared to adults. An X signifies that there were no significantly activated voxels found in the pre-designated ROI.*

ROI		Adults			Control Children			DD-Children		
		t	voxels	overlap	t	voxels	overlap	t	voxels	overlap
Left	EVC	5,23	11808	0.96	4,18	2729	0.00	3,64	6224	0.63
Right	EVC	4,80	10394	0.98	4,19	2406	0.00	4,05	3806	0.77
Left	OP	3,60	4072	0.83	3,98	3335	0.62	3,10	118	1.00
Right	OP	x	x	x	4,52	8938	0.15	x	x	0.92
Left	P-IPS	4,48	7038	0.98	4,04	6622	0.30	4,03	7419	0.81
Right	P-IPS	3,62	589	1.00	4,48	9546	0.41	3,74	7580	0.87
Left	A-IPS	4,26	6557	0.93	4,26	6557	0.57	4,07	10246	0.60
Right	A-IPS	5,59	16450	0.32	4,43	13269	0.46	3,64	8764	0.29
Left	SFG	4,67	7334	0.14	4,29	1500	0.18	4,05	6205	0.50
Right	SFG	5,40	12402	0.92	4,58	5625	0.42	3,77	5968	0.20
	SMA	3,72	2080	0.77	4,15	7166	0.06	4,52	9410	0.49
Left	ACC	x	x		x	x		x	x	x
Right	ACC	x	x		x	x		x	x	x

Table SIII.1.6. *Extent of significantly activated voxels and averaged t-values during the ADD-task and the proportion in which it overlapped with the VSWM-task. In contrast to the VSWM-task, dyscalculics often portray wider areas of significantly activated voxels, but T-values are all lower when compared to typical children. An X signifies that there were no significantly activated voxels found in the pre-designated ROI.*

Summary and general discussion

Summary of empirical findings

The work described in this thesis consists of a wide-ranging exploration on the link between numerical quantities and space. First, we investigated the relation between number processing and spatial processing in the light of the mental number line hypothesis. In doing this we have focussed on the nature of visual processing, specifically considering attention VSWM and consciousness and the interactions these aspects have with numerical and spatial processes.

In the first two experiments we describe replication-studies of seminal papers in the existing literature. Firstly, we implemented a study which aimed to replicate and extend the findings on the SNARC-effect as described by Dehaene, Bossini, and Giraux (1993) by implementing an experiment utilising a joystick we instructed participants to make movements to the left and right, using either their left or right hand and found that the SNARC-effect seems to be specific to the right hand in a right-handed population. In doing so we added a small contribution to the existing literature on the influence of the SNARC-effect on motor-planning as previous studies found influences on pointing (Fischer, 2003; Ishihara et al., 2006) and eye-movement (Fischer, Warlop, Hill, & Fias, 2004) and grasping (Andres, Davare, Pesenti, Olivier, & Seron, 2004). In this experiment we show that the association between numerical magnitude and used effector is diminished when participants need to make a lateral motion using a single hand. In this case there is no longer a bias for the left or right hand, but only for leftwards or rightwards motion.

The second replication study aimed at capturing the attentional SNARC-effect as described by Fischer, Castel, Dodd, and Pratt (2003). In three separate experiments tasks involving the detection of lateral stimuli after the presentation of central number cues, we expected to observe faster detection of targets on the left/right side of space when presenting participants with small/large numbers. This study was unable to replicate the attentional SNARC effect due to a lack of power and the possibility that the task did not require active processing of the presented Arabic digit.

This initial failure to replicate attentional SNARC effects led us to develop a novel feature in the testing of number-space interactions. For the following two experiments, which both introduce novel paradigms into the study of number-space associations, we adapted the classical use of Arabic digits as passively viewed number-cues by adding a control-question at the end of each trial, asking participants to judge either the parity or magnitude of the presented number-cue. This was done to ensure that participants would have to processes and remember the digit and it turned both these experiments into a working-memory task. With this instruction we wanted to make sure that participants processed at least these two semantic aspects of the number cues and we aimed to enhance the attentional cueing power of the Arabic Digits.

In the first of these newly developed behavioural studies we briefly presented a single Arabic digit before the onset of a line-bisection task. In this experiment we did find a spatial bias towards the left for low numbers and a bias towards the right for high numbers, as a function of number magnitude. However, when numerical information processing was diminished due to the presence of a visual mask, the spatial bias (and therefore the underlying modulation of attention) disappeared, leaving us to conclude that spatial associations of numerical magnitude might rely on conscious processing.

The second original study that successfully found an attentional SNARC-effect used binocular rivalry to suppress conscious perception. By briefly flashing a contrasting stimulus in each eye, we were able to suppress two lateral stimuli from being consciously perceived for up to several seconds. We found that the presentation of a single Arabic digit can facilitate a return of the supressed stimulus on the side of space that is congruent with the digit's numerical magnitude (e.g. faster return on the left for low and faster return on the right for high numbers).

In the final study that we present in the current work, we took a different approach to describing spatio-numerical associations. By examining how network-activations of children with Developmental Dyscalculia compared to those of typically developing children and adults under an arithmetic (addition) and VSWM-task during an fMRI-experiment we were able make inferences about the recruitment of resources in these two conditions. Consequently, we found diminished network-activations for the children with DD compared to the control-children, indicating a higher amount of variability in recruiting the areas involved in the task or, alternatively, a lesser amount of recruitment. Furthermore, we found that when participants were presented with a grid in the VSWM-task which was hypothesized to make the task easier, we found that children with DD show specific differences in the anterior cingulate cortex and early visual cortex, which are further elaborated below.

Reflections on the role of spatial attention in numerical processing and number-space associations.

The findings of both the binocular rivalry study as well as the masking study are in line with the MNL hypothesis and cannot be fully reconciled with proposals that go against the idea of a MNL as a representation of numerical magnitude (Hubbard, Piazza, Pinel, & Dehaene, 2005). Gevers, Verguts, Reynvoet, Caessens, and Fias (2006) proposed a computational model to account for the SNARC effect. This model consisted of three layers where the bottom layer represents numerical information and the upper layer represents response alternatives. The middle layer is responsible for conceptually categorizing numbers as small/large, odd/even, or any given category that is required by the task. These categorical representations are then associated with their corresponding alternative on a task-dependent response dimension. Consequently, a number that is categorized as small or large will first activate an abstract spatial code such as “left” or “right” before activating a response. Similarly, Proctor & Cho (2006) argued that the SNARC effect is a result of intermediate categorisation of numerical cues as high and low or odd and even. As long as stimuli can be coded on a polar level (either positive or negative) a similar location-coding will occur. Both these explanations are in line with a response-discrimination account of spatial associations (Lammerteyn, Gevers, Notebaert, Verguts & Fias, 2003; Santens & Gevers, 2008; Göbel, Johansen-Berg, Behrens, 2004) and speak against an account of the SNARC-effect that explains the spatial associations due to a direct mapping of a mental number-line onto visual space. Although the argument for the existence of response- and category-based spatial mapping is highly solid, the results in the current work cannot be accounted for by these frameworks. Indeed, the critical number-space biases were observed despite the fact that some of our experimental paradigms did not require any dichotomous encoding of numbers or space (e.g. II.3, Experiment 3 on binocular rivalry). In contrast, the present findings rather seem to indicate the existence of a mechanism that would better considering the mental number-line as a direct map of visuo-spatial coordinates.

In both the masking and the disrupted binocular rivalry experiments the numerical information of the remembered digit was irrelevant to the spatial task. This was also the case for other studies employing an attentional SNARC-effect (e.g. Dodd, 2011; Dodd, Van der Stigchel, Leghari, Fung, & Kingstone, 2008; Galfano, Rusconi, & Umiltà, 2006; Goffaux, Martin, Dormal, Goebel, & Schiltz, 2012; Ranzini, Dehaene, Piazza, & Hubbard, 2009; Ristic, Wright, & Kingstone, 2006). Given the different types of contexts in which these effects occur it is unlikely that the spatial mapping is solely due to a polarisation of response-options.

However, for both the experiments the digit was relevant for a control question which required participants to answer on either the parity or the magnitude of the presented digit. Since the control question was unknown to the participant (e.g. the participant did not know whether they had to answer on the magnitude or parity) it was very improbable that they categorised digit-cues ad hoc as odd vs. even or low vs. high. Even if participants would have adapted such a strategy in order to answer the control question, they would have needed to place each digit in two categories simultaneously (i.e. a two is both even and low). Given that the stimuli 1, 2, 8 and 9 contain two high numbers, two low ones, two odd ones and two even ones in a counter-balanced fashion, we would have expected that if the spatial association would have depended on polarisation due to placing them in the parity or magnitude-categories this would have obstructed the spatial performance in these tasks.

Lastly, in experiment three of the binocular rivalry study we found that vocal responses that were independent of any spatial association (e.g. saying 'ti' or 'to' for a first-return of triangle or star, with responses counterbalanced between participants) still elicited a higher proportion of first-returns on the left for low numbers and on the right for high numbers. This indicates that even when there is no spatial association whatsoever required for the processing of the task, the magnitude of a single digit still causes a bias that is congruent with the mental number-line.

Furthermore, during the masking-study we found that spatial bias vanished when a digit was successfully masked while the ability of participants to answer on parity or magnitude stayed intact. This indicates that the spatial activations that are associated with the numbers are, at least partially, separated the core numerical semantic information that they convey.

In conclusion, even though spatio-numerical associations are shown to be heavily context dependent, there seems to be evidence that spontaneous mapping places numerical information on a horizontal axis moving from left to right. A likely mechanism that would explain both types of findings is the existence of both bottom-up as well as top-down processes, where an initial bottom-up process favours a MNL, but this is easily diminished by top-down processes involving strategies and task-instruction. Given the arguments mentioned before, the most likely contender for supplying top-down modulation are working-memory resources.

However, I believe that the vast amount of flexibility of WM should not be over-simplified to solely be described as the handling of sequences. Things like operational scripts due to task-instruction, VSWM and verbal repetition should be taken into account when describing the contextual influences that surround associations between numbers and space (e.g. Georges, Schiltz and Hoffmann, 2015).

Reflections on the role of consciousness in number processing and number-space associations

A characteristic of the two attentional-SNARC studies concerned the role of conscious versus unconscious processing with relation to numerical information. Part of the current explanations with regards to consciousness revolve around the integration of information. According to Baars' global workspace theory, input from different sensory modalities and other conscious non-perceptual systems (such as the phonological loop) need to share a common space in order to become conscious (Baars, 1988, 1994, 2004). This has been extended by the Dehaene-Changeux computational model which is based on a neural network accounting for preconscious, unconscious and conscious phenomena (Dehaene & Changeux, 2003). It predicts that when stimuli or neurological events are powerful enough in order for them to pass their information on to an extended network (referred to as a global workspace) the owner of the network becomes conscious of the information that was passed on. Both the binocular rivalry and masking studies can be explained in the context of this model. As mentioned in the discussion of the study using masking to interfere with spatial bias, the spatio-numerical association seems to depend on this global workspace activation. When the digit is successfully masked (and therefore remains unconscious) its information is not shared with the network that makes the spatial association, which in turn prevents an attentional modulation from happening. In the binocular rivalry study we observe the other side of the coin for this model. In this case the Arabic digit is perceived consciously, meaning its information exists in a global workspace. Therefore it is able to cause an attentional shift, which will in turn fight cross-inhibition in the early visual cortex and cause the return of a lateral stimulus to the global workspace and enables conscious perception.

Reflections of the role of visuo-spatial working memory in developmental dyscalculia

The final study consisted in an event-related fMRI experiment comparing children with developmental dyscalculia to typically developing children and adults. We presented these three populations with an addition and a VSWM-task. During these tasks, people were asked to mentally add (addition) or remember the positions (VSWM) of consecutively presented patterns. In both of these tasks we manipulated the presence of an aiding visual structure (grid) that surrounded potential locations, which was hypothesized to only help with the task in the VSWM-condition.

We found that the fronto-parietal network activated by the task is influenced differently by the presence of a grid in the VSWM task for children with DD than in typical children and adults. Specifically, DD children showed significantly higher ACC activation than both control groups in the no-grid condition. At the same time, the grid presence/absence did not significantly affect BOLD responses of adults and control children in this frontal region. Conversely, removing the grid significantly decreased activation in early visual cortex for both control groups, but not for the DD children.

We argued that these results either indicate a deficit in bottom-up processing of visual information (reflected by a lack of response to the grid presence/absence in the visual occipital cortex) or a lack of executive control that causes inefficient top-down modulation of incoming information (reflected by an increased anterior cingulate response). In the latter case, the atypical directing of visuo-spatial attentional resources would be a likely explanation of why children with DD show different patterns of activation in the early visual cortex.

General considerations

The fact that children with DD show a heightened activation in the early visual cortex in the absence of a grid offers an interesting angle for interpretation when compared to the binocular rivalry and masking study. In the masking study we find evidence that the spatial association for numbers is diminished due to the presence of a mask, giving an indication that the link between numbers and space is dependent on intact, conscious visual processing of number symbols. When looking at the children with DD we see a different pattern of activation in areas that are involved in visual processing during a spatial WM task. Both these results reaffirm the relation between numerical/mathematical and spatial processes and suggest that accurate visual processing might be crucial in establishing this link. Similarly the results using disrupted binocular rivalry indicate that early visual processes are affected by the processing of numbers. If the faster return of a suppressed stimulus is due to the shifting of visuo-spatial attention, these shifts have to be caused by the numerical information. Consequently, the early visual processing that occurs (in this case resolving rivalry) are inherently affected by the numerical information conveyed by an Arabic digit.

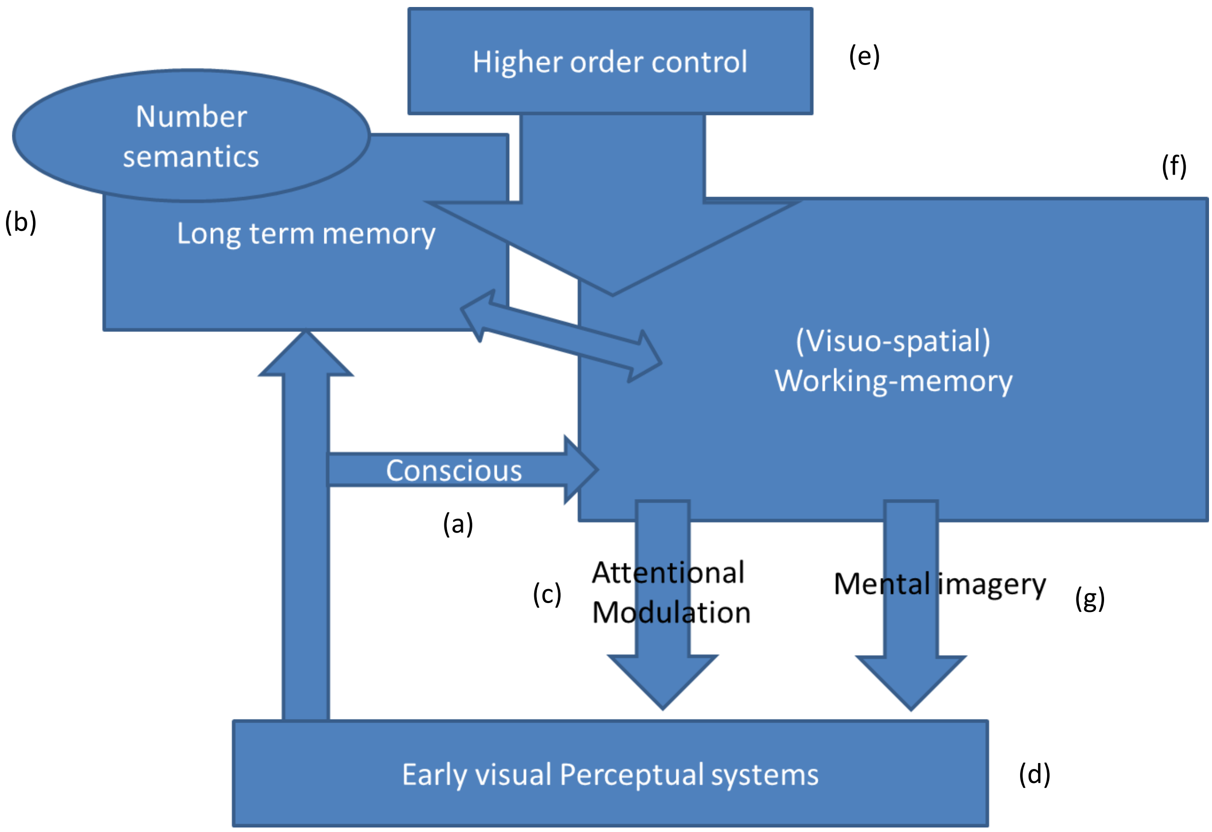

Figure SGD1. Summary of implications found in the current manuscript. We confirmed that number-space associations can influence early visual perceptual systems and depends on conscious processing that is separate from number semantics such as the parity or magnitude status of Arabic Digits. Furthermore we found that VSWM seems to influence early vision and both are probably affected by higher order (executive) control. As an alternative we propose that VSWM influences early vision due to mental imagery.

In summary the current manuscript proposes the existence and interplay of several mechanisms with regards to the processing of numerical information (Fig. SGD1). In an experiment using visual masking we found evidence that number-space associations are dependent on conscious processing (a) and seem to be separate from number semantics (i.e. classifying a non-conscious digit as high/low or odd/even) (b). In the context of working-memory the description an episodic buffer is described as being accessed through consciousness. As it is the episodic buffer which is proposed to integrate information from different sources such as long-term memory and perception, it seems logical that the results from this experiment might be due to an interplay between numerical processing and the episodic buffer (Baddeley, 2000). This would entail that separately from the semantic number-information, the episodic buffer integrates the spatial association to magnitude-information,

Furthermore, we found that the influence over early visual processes (c) due to number-space associations can modulate the amount of time that a stimulus remains suppressed after making use of the DRE. This suggests that attentional modulation due to number-space associations biases these early perceptual processes (d) and that therefore a mechanism exists that influences perception based on numerical magnitude. Finally, in a study that compares children with DD to typical children and adults, we found another influence on early vision related to numerical processing, but this time it was either due to executive control (e) over VSWM (f) or mental imagery (g) , suggesting that DD might be paired with either perceptual deficits or a lack of higher order control.

Conclusion and future prospects

Naturally, the current work does not provide an end-all argument to the current discussions. However, from our results we conclude that despite the fact that associations between numbers and space can take many forms and alternative accounts, there is no reason to disregard the mental number-line hypothesis as of yet. Indeed we offered evidence that cannot be accounted for by either polarity, response selection or WM-order explanations of spatio-numerical association. Future research will have to focus on the way context-dependency and strategies can affect preferential bottom-up associations at a fundamental level and investigate the mechanism by which it can override it.

A further issue that is not present for in the current work and would offer an interesting perspective for future study is to explain in which way power is given to a certain magnitude (e.g. why the SNARC- or attentional SNARC effects are stronger for a 1 and 9 than for a 2 or 8). For both attentional modulation and accounts of spatio-numerical associations that employ motor-tasks, there are stronger effects for the more extreme magnitudes, but as of yet I have not found a single empirical account of why this occurs.

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"A word to the wise… is infuriating"

-Hunter S. Thompson.

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Villmols Merci

Dennis