

INTERACTIONS BETWEEN NUMBERS AND SPACE –
NEUROBEHAVIOURAL EVIDENCE FROM CHILDREN AND ADULTS

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für meine Eltern

"Das Studium und allgemein das Streben nach Wahrheit und Schönheit ist ein Gebiet,
auf dem wir das ganze Leben lang Kinder bleiben dürfen."

Albert Einstein, *The Human Side*

SUMMARY

Mental number representations were examined in this thesis by asking participants to compare either numerical or spatial distances of visually presented number triplets (e.g. 57 64 92), a so-called “numerical landmark test”. Varying numerical and spatial distances independently resulted in neutral, congruent, and incongruent conditions. This paradigm was employed in classical reaction time (RT) experiments examining adults (*Study 1*) and children (*Study 2*) as well as in a neurofunctional investigation using high-resolution functional magnetic resonance imaging (*Study 3*).

In *Study 1* the comparison of numerical distances was influenced by the spatial alignment of the numbers (responses were facilitated on congruent trials and interference effects were present on incongruent trials), representing a so-called “distance congruity effect” (DCE). This finding was taken as evidence for a spatial representation of numbers in form of a so-called “mental number line”. No such interaction of numerical information with the spatial decision was observed. These asymmetric findings might be interpreted in terms of relative speed of information processing for the two dimensions or in terms of a parasitic representation of numbers on spatial representations, meaning that established structures representing space are recruited for new uses like number processing.

In *Study 2* children at the age of 8-9 years also exhibited a DCE when being confronted with the numerical landmark test. Correlations between the size of the DCE and calculation abilities were found to be differently marked for girls and boys, leading us to assume that girls and boys in this age make use of different thinking styles in order to solve calculation problems. For boys, who may prefer visuo-spatial thinking styles, a spatial representation of numbers could be helpful when being confronted with addition or subtraction problems, whereas for girls preferring verbal thinking styles it might be even detrimental.

Finally, in *Study 3* a reflection of the DCE at the neural level was detected in a distributed network comprising parietal and frontal areas. Identifying brain areas coding for subtraction, visual motion processing, and saccades in the same participants, revealed that these activations comprised regions that code for

saccades and calculation. Thus, numerical-spatial interactions may be driven by a network subserving attentional shifts and saccadic eye movements, which might also be involved in calculation. Numerical cognition and calculation might therefore be conceived as operations on a mental number line akin to physical movements along a physical trajectory. In sum, these findings underline the notion that neural circuitries being involved in updating internal representations of space during eye movements have been “recycled” for accommodating numerical functions and operations (Dehaene & Cohen, 2007).

KURZFASSUNG DER DISSERTATION

In dieser Dissertation wurden mentale Repräsentationen von Zahlen untersucht, indem die Probanden mit einem sogenannten "Numerischen Landmark Test" konfrontiert wurden. Bei diesem Test sollten entweder die beiden numerischen oder die beiden räumlichen Distanzen innerhalb eines Zahlentriples verglichen werden (z.B. 57 64 92). Die numerischen und räumlichen Distanzen wurden unabhängig voneinander manipuliert, so dass die jeweils nicht zu beachtende Dimension entweder kongruent, neutral oder inkongruent gegenüber der relevanten Dimension sein konnte. Dieses Paradigma wurde in Reaktionszeitexperimenten mit Erwachsenen (*Studie 1*) und Kindern (*Studie 2*) sowie in einer hochaufgelösten funktionellen Bildgebungsstudie (*Studie 3*) angewendet.

In *Studie 1* zeigte sich ein deutlicher Einfluss der räumlichen Anordnung der Zahlen auf den Vergleich der numerischen Distanzen (erleichternde Wirkung in der kongruenten und erschwerende in der inkongruenten Bedingung). Dieser Kongruenzeffekt wurde als Hinweis für das Vorhandensein einer räumlichen Repräsentation von Zahlen in Form eines sogenannten „mental Zahlenstrahls“ betrachtet. Die numerische Information hatte hingegen keinen Einfluss auf den Vergleich räumlicher Distanzen. Diese asymmetrischen Befunde könnten einerseits auf eine unterschiedliche Bearbeitungsdauer der verschiedenen Dimensionen zurückgeführt werden. Auf der anderen Seite besteht die Möglichkeit, dass mentale Repräsentationen von Zahlen auf der Basis von räumlichen Repräsentationen entwickelt wurden.

Der oben beschriebene Kongruenzeffekt konnte in *Studie 2* auch bei Kindern im Alter von 8-9 Jahren nachgewiesen werden. Zudem zeigte sich ein Zusammenhang zwischen der Stärke des Kongruenzeffekts und visuell-räumlichen wie auch rechnerischen Fähigkeiten, welcher in Abhängigkeit vom Geschlecht der Kinder unterschiedlich ausgeprägt war. Dieses wurde darauf zurückgeführt, dass Mädchen und Jungen verschiedene Strategien nutzen könnten, um Rechenaufgaben zu lösen. Für Jungen, die vermutlich visuell-räumliche Strategien bevorzugen, könnte eine räumliche Repräsentation von Zahlen beim Rechnen hilfreich sein, wohingegen sie sich für Mädchen eher störend auswirken könnte, da diese vermutlich verbale Strategien bevorzugen.

In *Studie 3* konnte gezeigt werden, dass ein Netzwerk bestehend aus parietalen und frontalen Neuronenverbänden für das Zustandekommen des Kongruenzeffektes verantwortlich ist. Die Identifizierung von neuronalen Netzwerken, welche für das Subtrahieren, die visuelle Bewegungswahrnehmung und für Augenbewegungen zuständig sind, deutete darauf hin, dass die dem Kongruenzeffekt zugrundeliegenden Neuronenverbände beim Rechnen wie auch beim Bewegen der Augen aktiv sind. Interaktionen zwischen Zahlen- und Raumverarbeitung könnten folglich durch ein neuronales Netzwerk hervorgerufen werden, welches für die Verschiebung der Aufmerksamkeit und die Bewegung der Augen wie auch für das Rechnen zuständig sind. Somit könnten Rechenprozesse als Operationen auf einem mentalen Zahlenstrahl betrachtet werden, die physikalischen Bewegungen im Raum gleichen. Insgesamt unterstreichen diese Ergebnisse die Ansicht, dass Neuronenverbände, die in die ständige Aktualisierung internaler Repräsentationen von Raum während der Bewegung der Augen involviert sind, „recycled“ wurden, um numerische Funktionen und Operationen zu übernehmen (Dehaene & Cohen, 2007).

TABLE OF CONTENTS

1. Introduction	1
1.1 Theoretical background	1
1.1.1 Connections between number and space processing	1
1.1.2 Models of number processing	10
1.2 A sketch of the empirical investigations	16
2. Study 1	
The distance congruity effect – evidence for a mental number line	19
2.1 Introduction	20
2.2 Experiment 1	20
2.2.1 Method	20
2.2.2 Results	22
2.2.3 Discussion	26
2.3 Experiment 2	27
2.3.1 Method	28
2.3.2 Results	28
2.3.3 Discussion	30
2.4 Experiment 3	31
2.4.1 Method	31
2.4.2 Results	32
2.4.3 Discussion	34
2.5 General Discussion of Study 1	34
3. Study 2	
Spatial representations of numbers in children and their connection with calculation abilities	37
3.1 Introduction	38
3.2 Method	39
3.3 Results	41
3.4 Discussion	48
4. Study 3	
Numbers and space – evidence for a link from high-resolution fMRI	51
4.1 Introduction	52
4.2 Method	52
4.3 Results	56
4.4 Discussion	66
5. General Discussion	69
5.1 Summary of the main findings	69
5.2 Theoretical implications	70
5.3 Potentials of the numerical landmark test	82
5.4 Future directions	84
6. References	85
Appendix	103

1. INTRODUCTION

1.1 Theoretical background

1.1.1 Connections between number and space processing

In 1880 Francis Galton documented the first known examples of so-called “number forms” (Galton, 1880a,b). He described individuals, who consciously experienced visual-spatial images when they processed numbers. This peculiar phenomenon was subject to further investigations (see Patrick, 1893; Calkins, 1895; Phillips, 1897; Seron, Pesenti, Noël, Deloche, & Cornet, 1992) and despite discrepancies these studies showed that visualised numbers are by no means rare. Prevalence estimates range between 5 and 16% (see Sagiv, Simner, Collins, Butterworth, & Ward, 2006 for an overview). For most of us, however, mental number representations are implicit, meaning that they are not consciously accessible. But there is ample evidence deriving from behavioural, neuropsychological, and neuroimaging experiments, which gives reason to assume that numbers are represented mentally in form of a so-called “mental number line” (MNL) possibly going from left to right (at least in left-to-right reading cultures). In the following these lines of evidence will be discussed in detail.

Behavioural data

The proposal of a MNL was put forward by Restle (1970) to explain the finding that we are faster and more accurate in comparing two Arabic numerals with respect to their magnitude the farther apart they are (“distance effect”, see Moyer & Landauer, 1967). This pattern is similar to participants’ performance in discriminating stimuli according to other physical dimensions such as line length or pitch (e.g. Henmon, 1906). Accordingly, the comparison of both numerical and physical magnitudes follows Weber’s law, which states that (physical) discriminations are ratio-sensitive, meaning that our performance depends on the proportion by which magnitudes differ on the respective dimension.

The SNARC effect (“Spatial-Numerical Association of Response Codes”; Dehaene, Bossini, & Giraux, 1993) is taken as evidence for a left-to-right oriented

MNL. It indexes the association of numerical magnitude with left-right responses: when subjects are asked to classify numbers as even or odd (parity judgement task) or compare numbers with respect to their magnitude (magnitude comparison task), the left hand responds faster to smaller numbers than to larger numbers while the right hand responds faster to larger numbers than to smaller numbers. This effect is independent of handedness (Dehaene et al., 1993), and it also occurs when individuals are asked to respond by making saccades (Schwarz & Keus, 2004; Fischer, Warlop, Hill, & Fias 2004), by pointing (Fischer, 2003), by grasping movements (Andres, Davare, Pesenti, Olivier, & Seron, 2004), or by providing bipedal responses (Schwarz & Müller, 2006). It occurs even in tasks that do not explicitly refer to numerical magnitude of the presented numbers. Indeed, a SNARC effect could be found when participants were asked to judge the phonemic content of number words relating to the Arabic number presented (Fias, Brysbaert, Geypens, & d'Ydewalle, 1996), or when they had to determine the orientation of a triangle or a line superimposed on a digit (Fias, Lauwereyns, & Lammertyn, 2001).

Dehaene et al. (1993) explained the finding of a SNARC effect in terms of an irrepressible correspondence between the position of response modalities and the position of a respective number on a MNL. Although the association of numerical magnitude with response modalities is assumed to be automatic, it can be changed by contextual features. In particular, Dehaene et al. (1993; see also Fias et al., 1996) showed that associating numerical magnitudes with response hands depends on the numerical interval introduced in the experiment. When participants are asked to judge the parity of Arabic numbers in the interval 0 to 5 for example, the numbers 4 and 5 were responded to faster with the right hand and more slowly with the left hand. On the other hand, the numbers 4 and 5 were responded to faster with the left hand and more slowly with the right hand, when the same participants had to judge the parity of Arabic numbers in the interval 4 to 9. Moreover, Bächthold, Baumüller, & Brugger (1998) asked participants to judge the magnitude of numbers 1 to 11 (without the number 6) in relation to the standard 6, while the subjects had to mentally align the centrally presented stimulus number with the corresponding location on an imagined ruler or on an imagined clock. A regular SNARC effect (small-left and large-right associations) was found for subjects who conceived of the numbers as distances on a ruler, but the SNARC was inverted (small-right and large-left associations) for subjects who conceived of them as hours on a clock face.

Beside these contextual influences, associations of numerical magnitude and response modalities might also be determined by cultural factors, such as reading direction: individuals, reading from right to left tend to show reduced or inverted SNARC effects (Dehaene et al., 1993; Zebian, 2005; Shaki, & Fischer, 2008) and native Chinese speakers from Taiwan showed a small-top and large-bottom association for numbers written in Chinese characters, which appear predominantly with a top-to-bottom organisation in Taiwan (Hung, Hung, Tzeng, & Wu, 2008). In this context, it is important to note that the SNARC effect is not found exclusively for numerical stimuli, but may be elicited also by other culturally learned ordinal sequences, like letters, months and days of the week (Gevers, Reynvoet, & Fias 2003, 2004). These findings undermine the hypothesis that the SNARC effect reflects the association of response modalities and the position of a respective number on a MNL. Recently, Santens and Gevers (2008) reported evidence favouring an alternative explanation for the SNARC effect. In a magnitude comparison task, the authors departed from the usual bimanual left-right response setting. Instead, they introduced a unimanual response that could vary between close and far responses, i.e. participants had to judge number magnitudes (1, 4, 6, and 9) relative to a standard (5) by moving their index finger either to a close or to a far location. An association between numerical magnitude and response codes was observed with small numbers being associated with close responses and large numbers being associated with far responses, regardless of the movement direction (left or right). This is not in accordance with a direct mapping of numerical magnitude representations in form of a MNL to response locations, which should have led to associations between close responses and numbers that are numerically close to 5 (i.e. 4, 6) and associations between far responses and numbers that are numerically far (i.e. 1, 9). Santens and Gevers (2008) interpreted these results as favouring accounts that entail an intermediate step between number magnitude and response representations, in which numbers are categorized as either small or large (a computational model of the SNARC effect see Gevers, Verguts, Reynvoet, Caessens, & Fias, 2006; polarity correspondence account see Proctor & Cho, 2006; see also 1.1.2 Models of number processing). Based on this finding, it is questionable to take the SNARC effect as evidence for spatial representations of numerical magnitude oriented such as a MNL. Although Santens and Gevers (2008)

assume that the use of the MNL metaphor remains useful and that such a spatial representation of numbers may well exist.

The existence of spatial number representations is supported by the finding that perceiving numbers can cause a shift of spatial attention to the left or the right side, depending on the magnitude of the number (Fischer, 2001; Fischer, Castel, Dodd, & Pratt, 2003; Calabria & Rossetti, 2005; Lavidor, Brinksman, & Göbel, 2004). Fischer (2001) showed that presenting strings of uniform digits can evoke a bisection bias: when asked to indicate the midpoint of a digit string composed of digit 1 or 2, participants deviated to the left, while strings made of digit 8 or 9 gave rise to a deviation to the right. This phenomenon was also found when strings were composed of French number words instead of Arabic digits (Calabria & Rossetti, 2005). Similarly, bisection of horizontal lines flanked by different digits on each side, is systematically biased towards the larger magnitude number (Fischer, 2001; de Hevia, Girelli, & Vallar, 2006). Even the simple presentation of a digit can automatically draw attention to the left or the right side (Fischer et al., 2003): participants were presented with single digit numbers (1, 2, 8 or 9) at fixation, followed by a target in either the left visual field (LVF) or the right visual field (RVF) which they had to detect. The presentation of relatively small digits (1 or 2) facilitated the response to targets in the LVF, while relatively large numbers (8 or 9) gave rise to faster detection of targets in the RVF. Similar to the SNARC effect, this kind of number-mediated orienting could be completely reversed by merely asking participants to imagine a clock or a number line running from right to left (Ristic, Wright, & Kingstone, 2006) or by encouraging participants to shift attention to the left in response to large numbers and to the right in response to small numbers (Galfano, Rusconi, & Umiltà, 2006).

Recently it could be demonstrated that not only number magnitudes but also calculation processes seem to evoke spatial biases. Indeed, outcomes of arithmetic problems are systematically misjudged as a function of the operation (i.e. addition or subtraction). Larger outcomes than the actual one are preferred in addition problems and smaller outcomes than the actual one in subtraction trials (McCrink, Dehaene, & Dehaene-Lambertz, 2007; Knops, Viarouge, & Dehaene, 2009). Comparably, pointing to outcomes on a visually given number line is biased leftward after subtracting and rightward after adding (Pinhas & Fischer, 2008).

While most behavioural studies focusing on the interaction between number and space processing have been conducted in adults, indications of similar effects were also reported in children. In 1977 Sekuler and Mierkiewicz reported a distance effect in children. The strength of this effect was found to be decreasing with age. It was comparable to that of adults for children in fourth and seventh grade, and even more pronounced for children in kindergarten and first grade (Sekuler & Mierkiewicz, 1977). In addition, a study by Berch, Foley, Hill, & McDonough Ryan (1999) showed that as early as at grade 3, typically developing children exhibited the SNARC effect. In accordance with this finding, Siegler and Opfer (2003) as well as Siegler and Booth (2004) showed that primary school children could translate between numerical and spatial representations. On the one hand children were able to locate a given number at the appropriate position on a visual line and on the other hand they could assign the appropriate number to a given position on a visual line. Recently, de Hevia and Spelke (2009) demonstrated that the bisection of horizontal lines, flanked by different arrays of dots on each side, is systematically biased towards the larger magnitude in children prior to the onset of formal instruction. Moreover, comparing a group of children with combined visuo-spatial and numerical disabilities at the age of 7–12 years to a control group, which was matched for gender, age, and verbal intelligence, revealed a SNARC effect in the control group but not in the group with visuo-spatial and numerical disabilities (Bachot, Gevers, Fias, & Roeyers, 2005). Based on these results the authors assumed that the link between numerical and visuo-spatial disabilities might be due to an abnormality in representing numbers. In the same vein, Schweiter, Weinhold Zulauf, & von Aster (2005) expected that spatial representations of numbers might be associated with mathematical abilities. Examining second graders, they showed that the size of the SNARC effect was correlated marginally with math performance. Interestingly, a marginal positive correlation was found for boys, whereas a marginal negative correlation was observed for girls. The authors suggested that gender-specific thinking styles and problem-solving strategies might account for these differences.

Neuropsychological data

In the early 20th century the functional importance of visual and spatial processes for number comprehension and calculation was recognized based on clinical observations (e.g. Peritz, 1918). These observations were interpreted in

terms of the suggestion that number representations must imply visual imagination in space (Bergson, 1911) and that understanding numbers necessarily requires an approximate idea of their positions relative to each other (Wertheimer, 1912). In combination, these observations and assumptions led to the notion that calculation processes need to be visualised (Peritz, 1918). In accordance with this idea, Luria (1974) proposed that math and arithmetic have a quasi-spatial nature analogous to mental manipulations of concrete shapes but entailing abstract symbols. In his view solving addition and subtraction problems may require spatial processes. Subtracting 16 from 61 for example, demands to assign different meanings to the “1” and “6” in the two numbers depending on the respective position. Furthermore, so-called “borrowing” from the decade column in 61 is needed. Indeed, it has been demonstrated later that visuo-spatial disorders following brain damage in the right hemisphere often come along with errors in calculation. Typical errors include omission of digits or even of a column of digits (Hartje, 1987) and recently it has been suggested that difficulties in relying on a representation containing a spatial layout or schema for calculation might play an important role (Grana, Hofer, & Semenza, 2006).

Further supporting evidence for a connection between number and space processing is provided by studies examining patients with hemi-spatial neglect due to brain damage most commonly in the right hemisphere. These patients have difficulties in exploring the side of space contralateral to the side of the lesion. In some cases this phenomenon also extends to mental images (Bisiach & Luzzatti, 1978). With regard to numerical processing, it has been shown that neglect patients not only misplace the midpoint of horizontal lines (line-bisection task, Marshall & Halligan, 1989) to the right, but also deviate to the right when asked to state the midpoint number of numerical intervals (e.g. responding that 5 is halfway between 2 and 6, Zorzi, Priftis, & Umiltà, 2002). In addition, patients with hemi-spatial neglect are also slower at judging smaller numbers relative to a reference numeral than larger ones (Vuilleumier, Ortigue, & Brugger, 2004). These findings argue for a representational deficit concerning numbers located to the left of a reference point along a MNL. Similar effects could be induced temporarily in healthy subjects using transcranial magnetic stimulation (TMS) over right posterior parietal cortex (Göbel, Calabria, Farne, & Rossetti, 2006). Recently, a neglect patient with left-hemisphere damage to the posterior superior parietal lobe and a deficit in exploring the right side

of space has been described, who showed leftward deviations for numerical as well as for visual stimuli (Pia, Corazzini, Folegatti, Gindri, & Cauda, 2009). Thus, the notion of a mental number line might be more than a metaphor. As proposed by Zorzi and colleagues (Zorzi et al., 2002) number lines and physical lines might be functionally isomorphic. This proposal, however, has been challenged by a study reporting that physical and mental number bisection can dissociate after right brain damage (Doricchi, Guariglia, Gasparini, & Tomaiuolo, 2005), leaving open to what extent the metaphor of a MNL is a valid description of the mental number magnitude representation.

Joint deficits of number and space processing were also observed in patients with Gerstmann syndrome (Gerstmann, 1940). This syndrome involves acalculia, agraphia and spatial problems, such as left–right confusion and finger agnosia. It is typically associated with lesions of the left inferior parietal lobule (angular gyrus). However, this kind of symptom-association data has to be treated with caution because it could be merely due to anatomical proximity of functionally-distinct systems. Indeed, it has been shown that the defining features of the Gerstmann syndrome can dissociate (Benton, 1992).

Aside from this neuropsychological evidence deriving from patients with acquired brain lesions, examination of children and adults with genetic disorders resulting in visuo-spatial deficits (e.g. Williams-, Velo-cardio-facial- and Turner-syndrome) also underline the connection between number and space processing. It has been reported that impairments of visuo-spatial abilities seem to prevent the development of exact number representations in children with Williams syndrome (Ansari et al., 2003) and that children with Velo-cardio-facial syndrome have difficulties in comparing numerical magnitudes, executing calculation strategies and solving word problems (De Smedt et al., 2007). In agreement with these data, it has been shown that children with Velo-cardio-facial syndrome performed more poorly on tests of visual attentional orienting, visual enumeration, numerical magnitude judgements (Simon, Bearden, Mc-Ginn, & Zackai, 2005) and simple arithmetic (Eliez et al., 2001) than groups of typically developing controls. Moreover, women with Turner syndrome show impairments in number estimation, subitizing (i.e. automatic visual recognition of the numerosity of small sets of objects), and calculation tasks (Bruandet, Molko, Cohen, & Dehaene, 2004) accompanied by functional as well as

structural anomalies around the right intraparietal sulcus (Molko et al., 2003), suggesting a crucial role of this region in number and space processing.

Neuroimaging data

Brain imaging provides further support for a connection between number and space processing. Tasks requiring number processing or spatial transformations both activate structures within the parietal lobes (Hubbard, Piazza, Pinel, & Dehaene, 2005). While most studies of numerical cognition have been conducted in humans, a large proportion of studies concerning spatial processing was conducted in monkeys. Studies of numerical cognition indicated, that structures around the bilateral horizontal segment of the intraparietal sulcus (hIPS) might play a particular role for a quantity representation of numbers (Dehaene, Piazza, Pinel, & Cohen, 2003). The hIPS seems to be active during a large variety of number-related tasks, including calculation (e.g. Burbaud et al., 1999), number magnitude comparison (e.g. Pinel, Dehaene, Riviere, & LeBihan, 2001), or even in the absence of explicit number magnitude processing (e.g. Eger, Sterzer, Russ, Giraud, & Kleinschmidt, 2003). Activation in the hIPS seems to be associated with an abstract representation of numbers, since neurons in this area respond to changes in numerosity, irrespective of notation. Arabic numerals, number words, and even non-symbolic stimuli like sets of visual or auditory objects and events activate this region (Castelli, Glaser, & Butterworth, 2006; Eger et al., 2003; Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004; Piazza, Mechelli, Price, & Butterworth, 2006; Piazza, Pinel, Le Bihan, & Dehaene, 2007; Pinel et al., 2001). Additionally, a bilateral posterior superior parietal region (PSPL) - frequently extending into the precuneus - appears to play a role in attention orientation along the mental number line (Dehaene et al., 2003). Although this region is also active during calculation and number comparison processes, it is not specific to the number domain. Rather, these brain structures have been found to be involved in visuo-spatial tasks like attention orienting, eye movements, grasping, pointing, and mental rotation (Culham & Kanwisher, 2001; Culham & Valyear, 2006; Piazza et al., 2004; Simon, Mangin, Cohen, Le Bihan, & Dehaene, 2002; Zago et al., 2001).

Parietal structures, thought to be important for spatial transformations were also found along the IPS of the macaque brain. These structures have been divided into several subregions that represent space, among them area LIP (lateral

intraparietal) and area VIP (ventral intraparietal). Neurons in the macaque area VIP are concerned with polymodal motion processing (Bremmer, Schlack, Duhamel, Graf, & Fink, 2001; Grefkes & Fink, 2005) in predominantly head-centred coordinates (Colby, Duhamel, & Goldberg, 1993), whereas area LIP represents target positions in an eye-centred frame of reference (Colby, Duhamel, & Goldberg, 1995). LIP is involved in spatial updating (Duhamel, Colby, & Goldberg, 1992), which describes the fact that changing properties of incoming visual information are monitored to generate a continuously accurate representation of visual space. Moreover, LIP neurons are part of a network mediating saccades (Grefkes & Fink, 2005) and the locus of attention (Bisley & Goldberg, 2003). In this context Rizzolatti, Riggio, Dascola, & Umiltà (1987) proposed that orienting of attention and eye movements are controlled by common mechanisms and that an attention shift represents a voluntary prevention of an eye movement.

Putative homologue areas have been identified in the human brain (see Culham & Valyear, 2006 for an overview). A region of the posterior IPS, which is active when humans make saccades to targets in different locations in space, might be homologous to macaque area LIP (Serenó, Pitzalis, & Martínez, 2001). Whereas this macaque LIP is located on the lateral bank of the IPS, the putative human homologue hLIP lies medial to the IPS. Another similarity between LIP in the human and in the macaque brain is the involvement in spatial updating (Medendorp, Goltz, Villis, & Crawford, 2003). In contrast, regions of the human IPS that respond to motion in multiple sensory modalities are thought to be plausible homologues of area VIP (Bremmer, Schlack, Shah et al., 2001).

Based on these findings, Hubbard et al. (2005) proposed that numerical-spatial interactions arise from common parietal circuits for attention to external space and internal representations of numbers (for a similar proposal see Walsh, 2003). Interestingly, areas around the hIPS of the human brain (assumed to play a particular role in the quantity representation of numbers, see above) seem to roughly coincide with the putative human area VIP, which is consistent with the localization of numerosity-selective neurons in the monkey brain close to the VIP (Nieder & Miller, 2004). That is why there might be a quantity representation in area VIP, which is connected to area hLIP neurons involved in shifts of attention in the external world and perhaps also in shifts of attention along the mental number line (Hubbard et al., 2005). Indeed, an fMRI study by Fias, Lammertyn, Reynvoet, Dupont, and Orban

(2003) revealed that judgments about Arabic numbers, line lengths and geometric angles activate a common neural substrate in the parietal cortex. In line with the aforementioned assumptions, Fias and colleagues (2001) conceptualized this association of number and space processing in terms of the overlap between their neural implementations. Recent findings by Tudusciuc and Nieder (2007) seem to corroborate this view by showing that numerosity and length are encoded by functionally overlapping groups of parietal neurons in the monkey brain.

1.1.2 Models of number processing

In the following, models of number processing will be described. Several different models have been proposed (see Willmes, 2002 for an overview) but only some of them consider a link between numerical and spatial representations. As this link represents the central issue here, it will be focused disregarding other theoretical considerations in the field of number processing.

Triple-code model

The triple-code model of number processing (Dehaene, 1992; Dehaene et al., 1993; Dehaene & Cohen, 1995, 1997; Dehaene et al., 2003) proposes that numbers can be mentally represented in three different codes: a visual-Arabic number form, an auditory-verbal word frame, and an analogue magnitude representation. The visual Arabic code, in which numbers are encoded as strings of Arabic numerals, probably depends on ventral occipito-temporal structures belonging to the ventral stream (cf. Ungerleider & Mishkin, 1982). The verbal system represents numerals lexically, phonologically and syntactically. It engages left hemispheric perisylvian language areas, the angular gyrus as well as subcortical regions, including the basal ganglia and thalamic nuclei and is assumed to mediate retrieval processes for simple addition and multiplication facts. These visual and verbal codes are thought to be non-semantic and more related to the surface format of numerical input and output processes. Critical for our purposes is the analogue code, which provides a semantic representation of the size and distance relations between numbers and is supposed to rely on areas around the hIPS, bilaterally.

Dehaene (1997; Dehaene et al., 2003) supposed an initial prespecialisation of these brain circuits for number processing called “number sense”. Indeed, quantity processing seems to be present early on in infancy. Young children in their first year of life can discriminate collections based on their numerosity (Starkey & Cooper, 1980; Xu & Spelke, 2000). These early numerical abilities may be supported by a quantity representation, which relies on neural circuitries in parietal cortex initially developed for coding internal representations of space (“neuronal recycling hypothesis”, Dehaene, 2005; Dehaene & Cohen, 2007). Izard, Dehaene-Lambertz, and Dehaene (2008) supposed that this kind of quantity system predisposed for spatial and numerical transformations might be present since birth. After mapping this semantic representation onto words and symbols, it is assumed to serve as a foundation for the construction of higher-order arithmetical and mathematical concepts. It may be relevant for solving subtraction, larger addition and division problems. Moreover, it is conceptualized as an oriented and logarithmically compressed MNL (Dehaene, 1992, 2003). This assumption of logarithmic compression is based on the finding that response time in a magnitude comparison task follows a logarithmic function of the distance between the numbers. However, beside this compressed scaling assumption, other proposals on the internal structure of the MNL have been suggested. These will be discussed in the following.

Proposals on the internal structure of the mental number line

Instead of assuming that numbers are represented in form of a MNL, which is logarithmically compressed (“compressed scaling”; Dehaene, 1992), it has been proposed that the mental code for a number might be analogous to the magnitude it represents. For instance, if a given number activates a set of units on the mental number line, this set of activated units is a subset of the units activated for a larger number (“magnitude coding”; Zorzi & Butterworth, 1999). Figure 1 shows a graphical illustration of these different proposals.

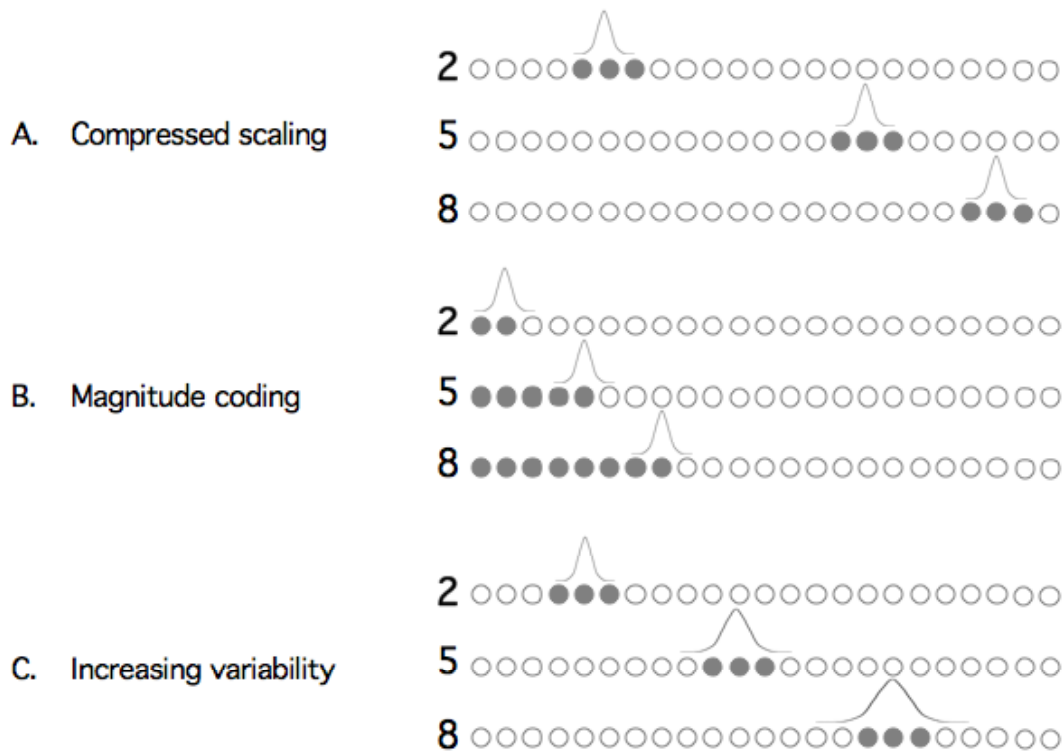


Figure 1. Graphical illustration of different proposals on the internal structure of the mental number line.

Moreover, another approach entails the assumption of increasing variability (Gallistel & Gelman, 1992). As can be seen in Figure 1, units close to the maximally activated unit (the unit over which the curve is centred) are also activated. Following the idea of increasing variability, the amount of co-activation depends on the size of the number, because standard deviations of the Gaussian curves that represent numerosities are supposed to increase with increases in the size of the number to be represented.

A connectionist model of numerical cognition

A neural network model avoiding the abovementioned assumptions of the internal structure of the MNL was proposed by Verguts, Fias, and Stevens (2005). This model instead assumes linear (not compressed) place coding representations with constant variability and consists of an input field and a number line field (see Figure 2).

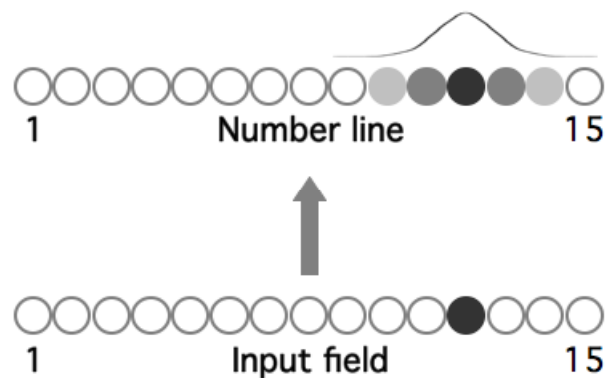


Figure 2. Graphical illustration of the internal structure of the mental number line as proposed by Verguts, Fias, and Stevens (2005).

In the input field different units represent different Arabic numbers. For example, unit 1 responds to the presentation of the (Arabic) number 1, unit 2 to number 2, and so on. Activation in the input field then spreads to the number line field. This field also consists of units for each number. As opposed to magnitude coding (Zorzi & Butterworth, 1999), each number activates an equal number of units on the number line (place coding). In addition, it is assumed that the number line is scaled linearly not logarithmically (Dehaene, 1992), resulting in equal distances between numbers on the number line. The model is further characterized by constant variability (instead of increasing variability; Gallistel & Gelman, 1992). As a result, activation functions are constant over different numbers. Although neighbouring units are co-activated, the activation curves have the same width for each number.

This model incorporates only numbers up to 15. In the view of the authors an extension of the model for larger numbers would result in fuzzier representations. They argue that these nonlinear mappings would derive from the lower frequency of larger numbers, observed in daily life (Dehaene & Mehler, 1992). Small numbers would be represented in an exact manner due to their high frequency, and large numbers in an increasingly fuzzier fashion. Hence, the properties of compressed scaling and increasing variability may well hold but only for larger numbers.

An extended version of this model was provided for a detailed conceptualization of the SNARC effect (Gevers et al., 2006). The model consists of three layers (see Figure 3).

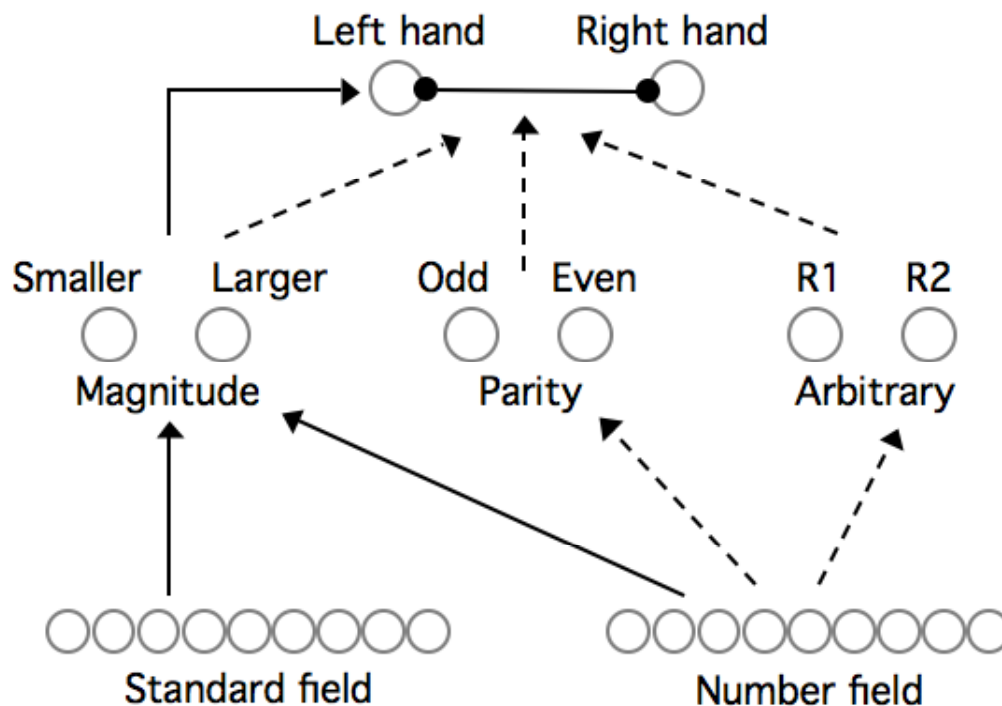


Figure 3. Graphical illustration of the model by Gevers, Verguts, Reynvoet, Caessens, and Fias (2006) explaining the SNARC effect for a parity judgment task, a magnitude comparison task, and a task where an arbitrary mapping is applied from number to response; R1 = Response 1, R2 = Response 2.

The bottom layer represents the number line field, which consists of a number field and a standard field. In the number field the presented target numeral is encoded and the function of the standard field depends on the respective task. It can code the internal standard to which the target numeral has to be compared in a magnitude comparison task or it codes the mean of the presented numerals in a parity judgement task. Each of these two fields is connected to the middle layer, in which numbers are always coded as either small or large. Depending on the task, additional fields can be activated in parallel, coding for e.g. parity (odd or even). The top layer codes a left and a right response. These two nodes can inhibit one another and one of them can initiate a response once a fixed threshold is reached. Due to this model, the SNARC effect arises because of a dual route from the middle layer to the response field: the first one constitutes an automatic route, which is triggered in any

numerical task. Here the node “smaller” projects to the response node “left” and the node “larger” projects to response node “right”. The second route is intentionally controlled depending on task instructions. It is assumed that more time will be needed to reach the response threshold if the automatic and the task-related route activate a different response hand. This dual-route architecture has been derived from conceptions for Stimulus-Response (S-R) correspondence effects (e.g. Kornblum, Hasbroucq, & Osman, 1990). These models incorporate two independent pathways for information processing. One of them is a relatively fast unconditional route that is activated automatically and the other one is a relatively slow conditional route that is dependent on task instruction. If both routes converge on the same response code (congruent condition), a response can be initiated relatively fast. If, on the contrary, both routes converge on opposing response codes (incongruent condition), reaction times are slower and errors are more frequent.

Most importantly, the model by Gevers and colleagues (2006) entails an intermediate step between number magnitude and response representations, in which numbers are categorized as either small or large. This assumption of a categorical number representation is in line with the aforementioned polarity correspondence account by Proctor and Cho (2006). According to this account, different polarities are assigned to different stimuli and responses depending on their relative saliency. The more salient stimulus and the more salient response are associated with the positive polarity “+” and the less salient response with the negative polarity “-”. Regarding the SNARC effect, both accounts predict an association of large magnitudes and right responses (i.e. both “+”) and of small magnitudes and left responses (both “-”). Thus, the SNARC effect would result from a correspondence between categorical number magnitude (or polarity) assignments and response representations.

In contrast, it has been proposed that both spatial as well as numerical magnitude information converge on a common representation, which is in turn associated with spatial responses. As mentioned above, Hubbard et al. (2005) proposed that numerical-spatial interactions arise from common parietal circuits for attention to external space and internal representations of numbers. They assume a quantity representation in area VIP, which is connected to area hLIP neurons involved in shifts of attention in the external world and perhaps also in shifts of attention along the mental number line. In accordance with this proposal, a

generalized magnitude system for numbers, space, and time was proposed by Walsh (2003), which will be described in the next section.

A theory of magnitude (ATOM)

Walsh (2003) attributes the quantification of time, space, and number magnitude to a single abstract magnitude representation. Based on the key role of parietal cortex in the transformation of object properties into action (Milner & Goodale, 1995), he assumed that metrics underlying temporal, spatial and numerical computations are translated into motor coordinates. In other words, the assumed magnitude system aims at solving issues like: “how long, how far or how many”. Consequently, Walsh proposed that interactions between time, space and number processing arise from their joint influence on the planning and execution of goal-directed movements. The neural correlate underlying these interactions is supposed to lie in the right inferior parietal cortex of the human brain. However, since exact calculation requires access to verbal representations, it is assumed that bilateral number representations emerged in inferior parietal cortex. According to Walsh, number representations are initially part of an undifferentiated magnitude system. Throughout development, these representations are progressively differentiated by interactions with the outside world.

1.2 A sketch of the empirical investigations

Three different studies will be addressed in this thesis. All of these studies elaborated mental number representations. The main goal of *Study 1* was to provide further evidence for the assumption of a number representation in form of MNL. We investigated the hypothesized representation by presenting number triplets spatially and numerically (always in ascending order) arranged as a line. Varying numerical and spatial distances independently resulted in neutral, congruent, and incongruent conditions (see Figure 4).

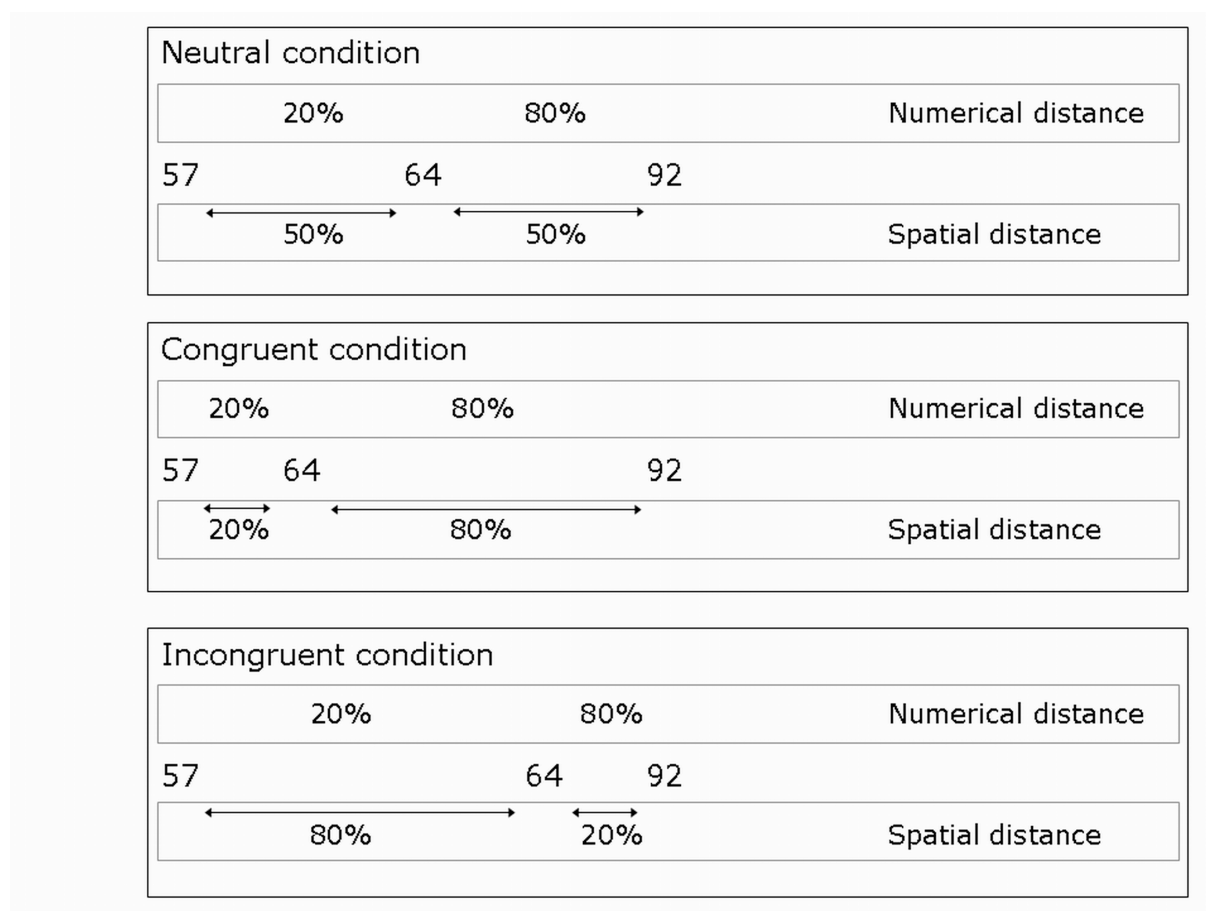


Figure 4. Examples of the spatial arrangement of one number triplet in the numerical landmark test. The triplet is shown in the neutral condition for the comparison of numerical distances (top), the congruent (middle) and incongruent (bottom) condition.

Participants had to compare either numerical or spatial distances of the different number triplets. In analogy to Milner, Harvey, Roberts, and Forster (1993) this task is called “numerical landmark test”. If the mental representation of numerical magnitude entails a spatial organization as a line, congruity or incongruity with the external spatial arrangement of the numbers might become response-relevant. That is, if the external spatial arrangement of the numbers coincides with the assumed spatial arrangement of the mental number magnitude representation this might result in a facilitation of decisions concerning the numerical relations between the constituting numbers. If, on the other hand, the external spatial arrangement of the numbers did not coincide with the internal layout, we expected responses to be

slowed down and to be more error prone. These predictions and related questions were tested in three different studies.

Study 1 comprised three experiments. In Experiment 1 participants had to indicate the side with the larger numerical or spatial distance, while participants were only asked to compare the numerical distances (not the spatial ones) and instructed to indicate the side that contained the smaller numerical interval in Experiment 2. Instead of using number triplets consisting of two-digit numbers (Experiment 1 and 2) single-digit numbers were presented in Experiment 3.

In *Study 2* the numerical landmark test was used to assess spatial representations of numbers in children at the age of 8-9 years. Children had to indicate the side of the larger numerical distance within number triplets consisting of two-digit numbers. Besides, visuo-spatial and calculation abilities of each child were assessed in order to reveal possible connections between these proficiencies and spatial representations of numbers.

Finally, *Study 3* examined the neural underpinnings of spatial number representations by high-resolution fMRI. We tried to identify neural networks subserving subtraction, visual motion processing or saccades. In addition, the abovementioned paradigm revealing behavioural interactions between the processing of numerical and spatial distances was used. Being able to identify the neural correlates of this interaction offered the chance to look for possible overlaps with hLIP, VIP and hIPS areas.

2. STUDY 1

THE DISTANCE CONGRUITY EFFECT – EVIDENCE FOR A MENTAL NUMBER LINE

(Co-authored with A. Knops and K. Willmes)

2.1 Introduction

Indications of a number representation in form of a MNL were reported in the introduction. In sum, convincing behavioural evidence for this assumption is still missing, because none of the presented pieces of evidence is without contradiction. Concerning the SNARC effect, a finding that has been interpreted in terms of such a structure of mental number representations, evidence has been reported favouring alternative explanations (Santens & Gervers, 2008). Likewise, the finding that merely looking at numbers induces shifts of attention has been demonstrated not to be obligatory (Galfano et al., 2006), both fragile and flexible, and depended on the top-down spatial mental set (Ristic et al., 2006). As a result, the main goal of *Study 1* was to provide behavioural evidence for the assumption of a number representation in form of a MNL.

2.2 Experiment 1

2.2.1 Method

Participants

Twenty (19 right-handed, 15 female) participants (mean age 27.7, range 20-62 years) were tested.

Stimuli

The stimulus set consisted of 96 two-digit number triplets (plus 48 neutral triplets in the comparison task of spatial distances, see below) arranged horizontally. Figure 4 depicts an example of the layout and the manipulated factors. Numerical magnitude of the numbers increased from left to right for all triplets. None of the number triplets was part of a multiplication table or included decade numbers.

The spatial and numerical position of the middle number was varied independently. Therefore, numerical and spatial intervals could be congruent (e.g.

both intervals were smaller on the left side) or incongruent (e.g. numerically the left interval was larger while spatially the right one was larger). In neutral triplets either numerical or spatial intervals were identical. Three different numerical ranges (NR, i.e. numerical distance between the two outer numbers of a triplet) were chosen (NR = 15, 35, 45). Each NR contained four numerical distance-pairs (ND, i.e. numerical distance between the middle number and the outer numbers), expressed as percentages of the respective NR (ND = 20/80, 40/60, 60/40, and 80/20). For each NR by ND condition eight different number triplets were chosen, resulting in 96 different number triplets. Within (across) the three numerical ranges, number triplets were matched for problem size, parity, and number of decade crossings (problem size and parity). Three spatial ranges (SR = 5 cm, 7 cm, 9 cm; visual angles of 4.8°, 6.7°, 8.5°) and four spatial distance-pairs (SD = 20/80, 40/60, 60/40, 80/20) were used. Combining the 96 number triplets with these spatial variations (SR by SD) resulted in 1152 different stimuli, of which 576 were congruent and 576 were incongruent.

An additional set of 576 neutral stimuli was constructed for each task. In the numerical comparison task, the 96 number triplets described above were used in the neutral condition with all SR. The resulting 288 stimuli were presented twice to yield 576 neutral stimuli. In the spatial comparison task 48 new neutral number triplets with six different NR (14, 16, 34, 36, 44, 46; on average resembling the ranges in the numerical task) were constructed. The resulting 288 stimuli were used twice and matched for problem size, parity, and decade crossings within each NR and for problem size and parity over NR. The two-digit numbers had a visual angle of 0.5° in height (5 mm) and of 0.7° in width (7 mm) from a viewing distance of about 60 cm.

Procedure

Participants were randomly assigned to one of two tasks: numerical or spatial interval comparison. Participants had to indicate the side with the larger numerical (spatial) distance by lifting the left or right index finger from a custom-made response device. Accuracy and speed were equally stressed in the instructions. The 1728 trials were presented in 9 blocks of 192 trials. The trials were pseudo-randomized so that identical number triplets never followed each other and numerical (or spatial) distance pairs were not identical on 3 or more consecutive trials. From trial to trial the position of the two-digit numbers was slightly shifted on screen (from 0.04° to 0.6°).

The experiment was preceded by 12 practice trials and controlled by a PC (Intel® Pentium® Processor 1600 MHz) with Presentation® software (Neurobehavioral Systems).

A trial started with the presentation of a fixation cross for 500 ms. After the fixation cross had vanished, the target appeared for a maximum duration of 3000 ms unless the response terminated presentation earlier. After the trial ended, a black screen was presented for 500 ms, which served to separate consecutive trials from each other.

2.2.2 Results

Analyses of variance (ANOVA) and post-hoc tests employing a Bonferroni correction for multiple testing (t tests for dependent samples) were conducted separately for reaction time (RT) and error rate (ER). ER was arcsine-transformed ($2\arcsine\sqrt{ER}$) to better approximate normally distributed data. Huynh-Feldt epsilon (Huynh & Feldt, 1976) was used to correct the degrees of freedom in case of non-sphericity ($\alpha = 10\%$). Trials in which no response occurred were classified as errors. Responses below 200 ms were excluded from further analysis, as well as responses outside of an interval of ± 3 standard deviations around the individual mean. Trimming resulted in 0.6% of response exclusions. Table 1 provides an overview of the results.

Table 1

Mean reaction times (RT) for correct responses in ms and percentage of errors (ER) as a function of the factor congruity (congruent vs. neutral vs. incongruent) with standard deviations in parentheses.

		Congruent	Neutral	Incongruent
Experiment 1				
Numerical task	RT in ms	1466 (262)	1482 (260)	1516 (257)
	ER in %	9.7 (4.3)	13.7 (5.9)	17.9 (9.0)
Spatial task	RT in ms	403 (74)	403 (70)	403 (72)
	ER in %	3.2 (1.6)	2.8 (2.0)	2.7 (1.7)
Experiment 2				
Numerical task	RT in ms	1496 (185)	1527 (200)	1567 (211)
	ER in %	9.6 (3.4)	12.1 (3.9)	15.6 (3.7)
Experiment 3				
Numerical task	RT in ms	1016 (177)	1052 (185)	1078 (170)
	ER in %	2.2 (1.7)	3.5 (3.3)	5.2 (3.4)
Spatial task	RT in ms	391 (32)	389 (32)	389 (31)
	ER in %	2.6 (1.7)	2.2 (1.3)	2.6 (1.9)

Reaction time

A 3×2 ANOVA including the within-subject factor congruity (congruent, neutral, incongruent) and the between-subject factor task (numerical comparison vs. spatial comparison) was conducted. The two tasks differed significantly (numerical comparison: 1488 ms, spatial comparison: 403 ms; $F(1, 18) = 163.42$, $p < .001$), and a significant main effect for congruity ($F(2, 36) = 9.23$, $p < .01$, epsilon = .777) showed fastest mean RT for congruent and slowest mean RT for incongruent trials. This main effect was mediated by an interaction with the factor task ($F(2, 36) = 9.36$, $p < .01$, epsilon = .777). Separate ANOVAs for the two tasks with congruity as within-subject factor revealed a significant main effect for congruity only for the numerical comparison task (numerical comparison: $F(2, 18) = 9.66$, $p < .01$, epsilon = .784; spatial comparison: $F(2, 18) = 0.02$, $p = .98$), where RT for incongruent trials was significantly larger than for neutral ($p < .01$) and congruent trials ($p < .05$), as revealed by post-hoc paired-sample t tests. To illustrate the distribution of the

congruity effect over the whole range of latencies, Figure 5 depicts the cumulative density function of RT deciles (e.g. Ridderinkhof, 2002) for congruent, incongruent and neutral trials, respectively. According to visual inspection of the graphs, the congruity effect mainly arose between the fourth and the seventh response deciles (mean RT between 1300–1700 ms).

Error rate

A significant difference between the two tasks (numerical comparison: 13.8%, spatial comparison: 2.9%; $F(1, 18) = 36.60$, $p < .001$), a significant main effect for congruity ($F(2, 36) = 11.99$, $p < .001$, $\epsilon = .841$), and a significant interaction of congruity $\times$ task ($F(2, 36) = 26.62$, $p < .001$, $\epsilon = .841$) were observed. Again, separate ANOVAs for the two different tasks with congruity as within-subject factor revealed a significant main effect for congruity only in the numerical comparison task (numerical comparison: $F(2, 18) = 38.65$, $p < .001$, $\epsilon = .644$; spatial comparison: $F(2, 18) = 1.40$, $p = .27$): post-hoc paired-sample t tests revealed the following order of error rates, with all differences between conditions being significant: congruent < neutral < incongruent (incongruent - congruent: $p < .001$, incongruent - neutral: $p < .01$, neutral - congruent: $p < .001$). As can be seen from the conditional accuracy function in Figure 5 (Ridderinkhof, 2002) the congruity effect based on error rate mainly arose in the second and between the sixth and the ninth response accuracy deciles (mean RT between 1100–2100 ms).

In sum, these results suggest that spatial intervals between the three numbers of a triplet indeed influenced performance in the numerical comparison task in the form of a distance-congruity effect (DCE). No influence of numerical distance on performance in the spatial task was observed.

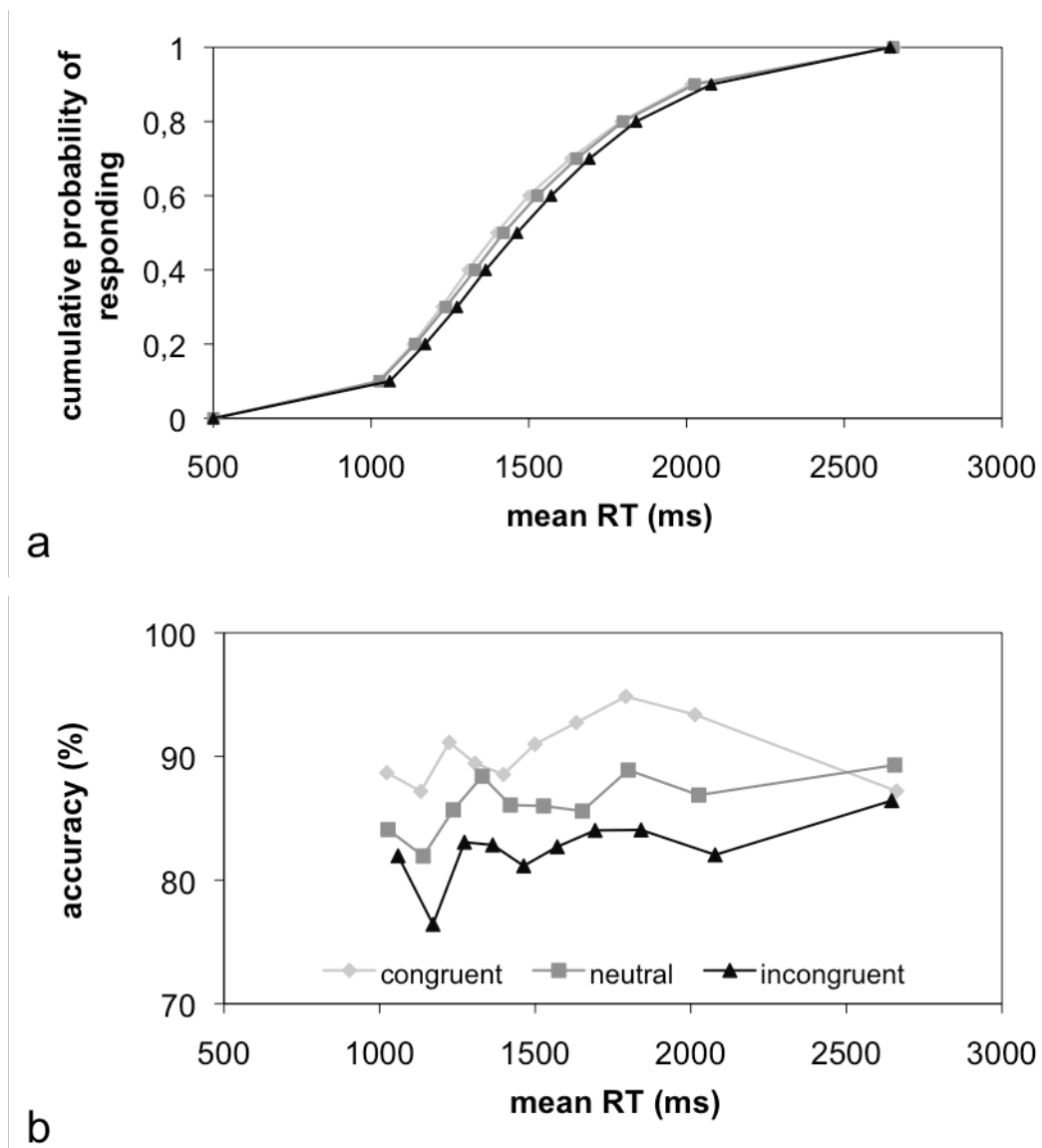


Figure 5. Conditional accuracy functions (a) and cumulative density functions (b) for Experiment 1. Cumulative density functions were approximated by plotting separately for congruent, neutral, and incongruent conditions the cumulative probability of responding as a function of mean RT (only correct responses) for each of the ten response speed deciles. Conditional accuracy functions were approximated by plotting separately for congruent, neutral, and incongruent conditions accuracy as a function of mean RT (only correct responses) for each of ten response accuracy deciles.

2.2.3 Discussion

Most importantly, an effect of congruity between numerical and spatial distance (DCE) was found in the numerical task: RT (ER) was fastest (lowest) with congruent and slowest (highest) in incongruent trials (see Table 1). No such interference was present in the spatial task. This supports the assumption that numerical magnitude information might be represented on a MNL.

Despite the evidence provided by Experiment 1, a major concern remains. Instead of attributing the observed effects to a(n) (in)congruity between external spatial distances and internal spatial distances on the MNL (i.e. numerical distances), one might assume that participants adopted a different strategy: for a given number triplet (e.g. 53__62_____98) they might first concentrate on the two numbers closest to each other and process their numerical distance (here: 9). Only subsequently they might shift gaze and attention to the third (“remote”) number (here: 98) and estimate the numerical distance to the middle number (here: 36), which is then compared to the first interval. This comparison either favors pressing the button located on the side of the remote number or a button press on the side of the first gaze. In the example provided here, the larger numerical interval is on the side of the remote number and therefore requires a right button press. If we reverse the spatial intervals in the above example (53_____62__98), the situation becomes incongruent, since the first gaze is on the right side of space and the shift of gaze and attention goes to the left. Some authors argue that the direction of attentional shift is the basis of the Simon effect (Nicoletti & Umiltà, 1994). The Simon effect describes the fact that responses are faster when the stimulus location corresponds to the location of the assigned response. In typical Simon experiments the attentional shift is a consequence of lateralized stimulus presentation. In our experiment the attentional shift might arise from the temporal order of numerical and spatial intervals considered by the participants. If attentional shifts are associated with the production of a spatial response code and this response code is congruent with the manual response required, we expect facilitation effects. If they are incongruent, we expect to observe interference effects. Thus the observed effects might be interpreted as an instantiation of the Simon effect. Most importantly, the assumed congruity effect

between numerical and spatial distances leads to identical predictions. In the present paradigm the “Simon effect hypothesis” is completely confounded with the assumed interference between numerical and spatial distance. However, a simple change of the instruction is sufficient to pit the predictions of the DCE approach against the predictions of this hypothesis. Instead of asking participants to indicate the larger of the two numerical intervals, we asked them to press the button corresponding to the smaller numerical interval. In the example provided above the larger numerical interval is located on the right side of space - the side of the spatially larger interval. Asking for the smaller numerical interval then requires overruling the assumed activated response code due to the attentional shift that occurred. This situation is incongruent in terms of the “Simon effect hypothesis” since the first gaze is supposed to be located at the two numbers on the left. However, with regard to the congruity of numerical and spatial intervals, the situation still is a congruent one. Both, numerically and spatially, the smaller interval is on the left. Observing the DCE comparable to the one obtained in Experiment 1 would provide evidence in favour of the interpretation of the DCE indicating a conflict between numerical and spatial distances rather than some generic conflict of spatial response codes. Finding the DCE effect reversed or diminished in size would indicate that the observed effects are (at least partially) an instantiation of the Simon effect.

2.3 Experiment 2

In Experiment 2 we tested the two explanations against each other. All methods and stimuli were identical to Experiment 1 with the following exception: participants were only asked to compare the numerical distances (not the spatial ones) and instructed to indicate the side that contained the smaller numerical interval.

2.3.1 Method

Participants

A group of 10 participants (10 right-handed, 8 female), not identical with those included in Experiment 1 was tested (mean age 24.5, range 21-29 years).

2.3.2 Results

The way of analyzing RT and ER was identical to Experiment 1. Trimming resulted in 0.5% of response exclusions. Table 1 provides an overview of the results for the numerical task.

Reaction time

A repeated measures ANOVA with the factor congruity (congruent, neutral, incongruent) revealed a significant main effect ($F(2, 18) = 20.13, p < .001$, epsilon = .696): RT for incongruent trials was significantly larger than for neutral ($p = .001$) as well as for congruent trials ($p < .01$). In addition, there was a marginal difference ($p = .055$) between neutral and congruent trials with larger RT for neutral trials. Visual inspection of the cumulative density function in Figure 6 revealed that the DCE mainly arose between the fifth and eighth response deciles (mean RT between 1400-1900 ms). The overall size of the congruity effect was comparable to that observed in Experiment 1, i.e. RT increased by 31 ms from congruent to neutral and by 37 ms from neutral to incongruent trials, respectively.

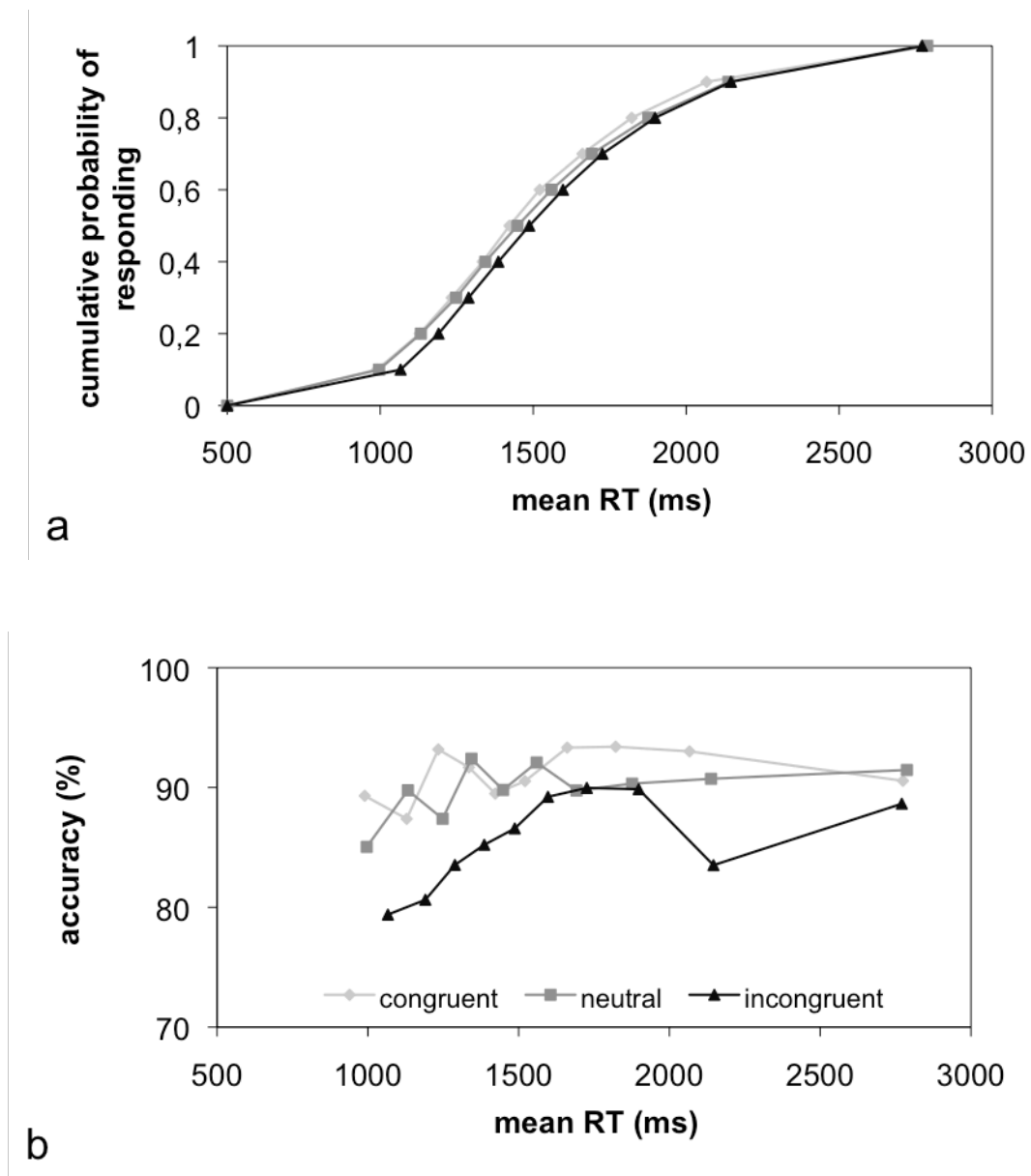


Figure 6. Conditional accuracy functions (a) and cumulative density functions (b) for Experiment 2.

Error rate

An identical ANOVA for arcsine transformed ER revealed a significant main effect of congruity ($F(2, 18) = 25.20, p < .001$). Paired t tests revealed the following order of conditions with all comparisons between respective conditions being significant: congruent < neutral < incongruent (incongruent - congruent: $p = .001$, incongruent - neutral: $p < .01$, neutral - congruent: $p < .05$). The conditional accuracy

functions in Figure 6 illustrate that the DCE based on error rate mainly arose in the first, the third and the ninth response accuracy deciles (mean RT between 1000-2200 ms).

2.3.3 Discussion

Experiment 2 was designed to test whether the observed DCE could be due to a conflict between assigned responses and response codes elicited by attentional shifts. To pit this “Simon effect hypothesis” against the assumed interaction between numerical and spatial distance, the same stimuli as in Experiment 1 (for the numerical comparison task) were presented to a different group of participants. Only instructions were changed: instead of indicating the larger of two numerical intervals, participants had to indicate the side of the smaller numerical interval. We were able to replicate the DCE with a numerical size of the differences between incongruent, neutral and congruent trials that resembled closely the results of Experiment 1. No evidence suggested a Simon-like spatial shift of attention as the origin of the observed effect. Thus, the results clearly support the idea that the observed behavioral conflict is due to conflicting information between the internal representation of numerical distances on the MNL and the external spatial position of the numbers.

Another objection to the findings in Experiment 1 is related to an asymmetry of the effects, with an influence of spatial information in the numerical tasks but no effect of congruity in the comparison task of spatial distances. This finding makes sense in the context of a relative speed account: the degree to which one factor (e.g. numerical distance) is able to influence the processing of the other factor (e.g. spatial distance) depends on the relative time necessary for processing the different factors. The attribute processed more slowly (e.g. numerical distance) should induce weaker or no interference on the factor which is processed faster (e.g. spatial distance; Schwarz & Ischebeck, 2003). Since spatial distances were processed much faster (numerical comparison: 1488 ms versus spatial comparison: 403 ms; see Table 1), it is plausible to assume that spatial distance information was available at a time when numerical distances were still being processed. Conditional accuracy plots and cumulative density function plots underlined this assumption by demonstrating

indications of a DCE in the numerical task from the early RT bins or deciles on. On the other hand, the numerical information was - on average - available only after 1500 ms, which might have prevented it from influencing spatial decisions, which were accomplished within 400 ms on average. The lack of interference of numerical information with the spatial intervals might therefore be due to the large difference in processing speed between the two tasks. We tested this latter hypothesis in a third experiment: we sought to decrease RT for the numerical decision by using single-digit instead of two-digit numerals. This should reduce both perceptual and cognitive load and accelerate the numerical decision, increasing the chance to interact with the spatial decision.

2.4 Experiment 3

2.4.1 Method

Participants

Twenty (19 right-handed, 15 female) participants different from the other samples (mean age 25.2, range 21-38 years) were tested.

Stimuli

Experiment 3 differed from Experiment 1 only in the use of single-digit numbers instead of two-digit numbers. The stimulus set consisted of twelve different triplets. Three different NR were used (5, 7, 8). Each NR contained four NDs (20/80, 40/60, 60/40, 80/20 for range 5; 28/72, 42/58, 58/42, 72/28 for range 7; 12/88, 38/62, 62/38, 88/12 for range 8), resembling the numerical distance-pairs used in Experiment 1, when averaged over ranges. For each NR × ND condition one number triplet was chosen. These triplets were matched for problem size. Crossed with spatial variations, this resulted in 144 different stimuli, 72 of which were congruent and 72 were incongruent. Additionally, 72 neutral stimuli were constructed for each task. In the numerical task, the twelve number triplets were used in combination with the three different SR and the neutral SD. The resulting 36 stimuli were used twice to yield 72 neutral stimuli.

For the spatial condition four neutral number triplets with neutral ND were constructed - one of these number triplets with NR = 4, two number triplets with NR = 6, and one with NR = 8. These number triplets were used twice to (a) provide 72 neutral stimuli, and (b) to yield the same numerical ranges (on average) as the ones used in congruent and incongruent stimuli. The numbers had a visual angle of 0.5° in height (5 mm) and of 0.4° in width (4 mm) from a viewing distance of about 60 cm.

Procedure

The procedure was identical to that of Experiment 1, except for the fact that the 216 different stimuli were repeated eight times in separate blocks.

2.4.2 Results

The way of analyzing RT and ER was identical to Experiment 1. Trimming resulted in 1.2% of response exclusions. Table 1 provides an overview of the results.

Reaction time

A 3×2 ANOVA including the within-subject factor congruity (congruent, neutral, incongruent) and the between-subject factor task (numerical, spatial) was conducted. Again, the comparison task of spatial distances led to faster RT than the comparison task comprising numerical distance (spatial comparison: 389 ms, numerical comparison: 1049 ms; $F(1, 18) = 134.71$, $p < .001$). RT was fastest for congruent and slowest for incongruent trials ($F(2, 36) = 22.68$, $p < .001$). A significant interaction (congruity $\times$ task: $F(2, 36) = 25.22$, $p < .001$) suggested that the main effect for congruity was only present in the comparison task of numerical distances.

Separate ANOVAs for the two different tasks with congruity as within-subject factor revealed a significant effect only for numerical comparison (numerical comparison: $F(2, 18) = 24.24$, $p < .001$; spatial comparison: $F(2, 18) = 1.98$, $p = .17$). Fastest mean RT was found for congruent and slowest mean RT for incongruent trials in the numerical task: Post-hoc paired-sample t tests indicated that the congruent condition differed significantly from the neutral ($p < .05$) and the incongruent one ($p < .001$). Additionally, the neutral and the incongruent condition

differed marginally ($p = .076$). The DCE mainly arose between the sixth and the ninth response deciles (mean RT between 1000-1600 ms, see Figure 7).

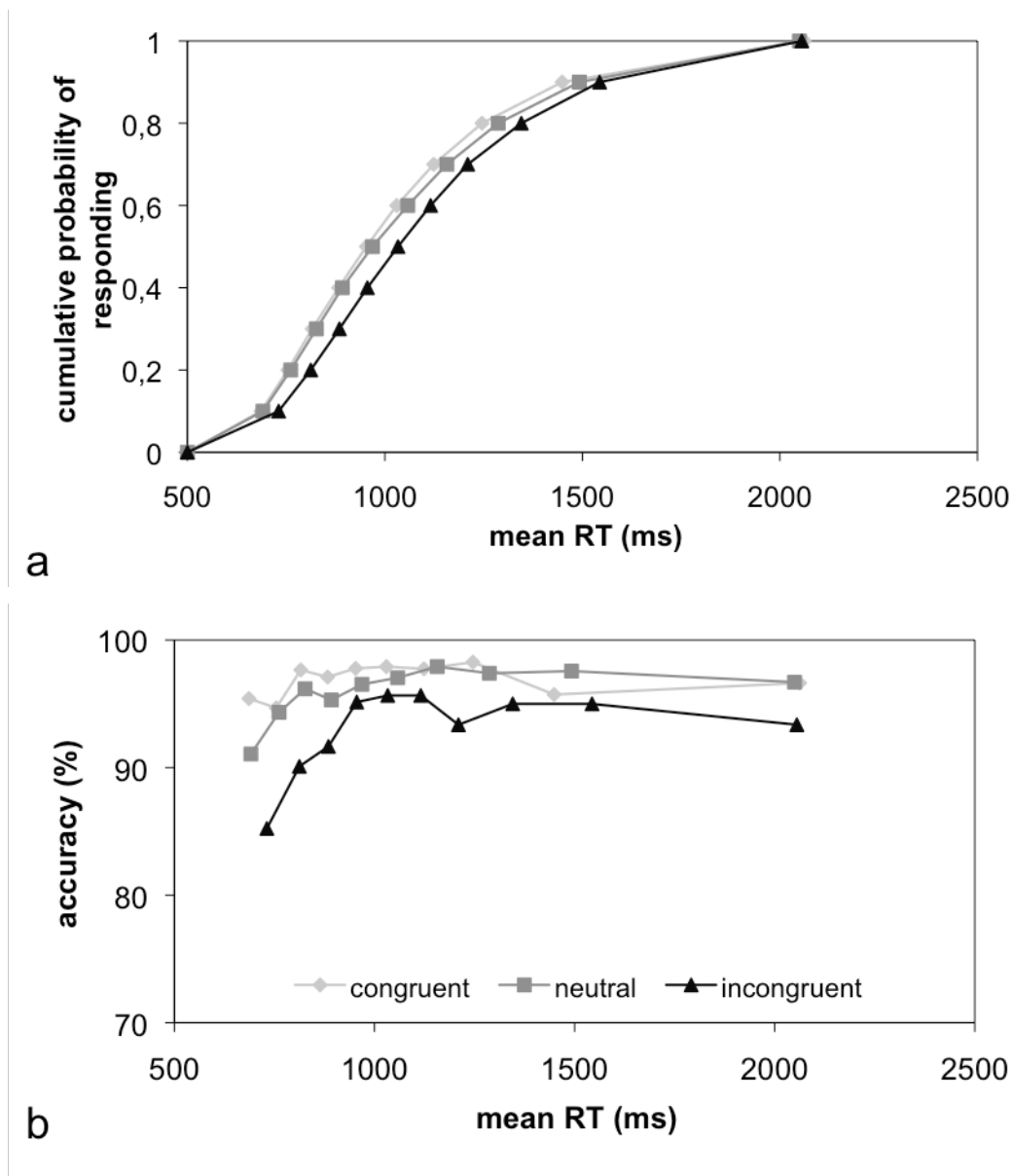


Figure 7. Conditional accuracy functions (a) and cumulative density functions (b) for Experiment 3.

Error rate

Analogous results were obtained for ER, except for the finding that there was no significant difference between the two tasks (numerical comparison: 3.6%, spatial comparison: 2.5%; $F(1, 18) = 0.29$, $p = .594$): A significant main effect for congruency

($F(2, 36) = 13.40, p < .001$), and a significant interaction (congruity $\times$ task: $F(2, 36) = 11.04, p < .001$) were present. Separate ANOVAs for the two different tasks with congruity as within-subject factor revealed a significant main effect for congruity in the comparison task of numerical distances ($F(2, 18) = 16.05, p < .001$) but not in the comparison task of spatial distances ($F(2, 18) = 2.75, p = .09$). In the numerical task the smallest ER was found for congruent and the highest for incongruent trials. Post-hoc paired-sample t tests indicated that the incongruent condition differed significantly from the congruent ($p = .001$) and the neutral one ($p > .01$). As can be seen from the conditional accuracy function in Figure 7, the DCE based on error rate mainly arose between the first and the sixth response accuracy deciles (mean RT between 700–1100 ms).

2.4.3 Discussion

The asymmetric DCE in Experiment 1 might have been due to the difference in processing speed between the two tasks. In Experiment 3 single-digit numbers were used to speed up numerical processing. Indeed, the numerical comparison was faster in Experiment 3 as compared to Experiment 1 (1488 ms vs. 1049 ms). Nevertheless, on average the spatial task was still performed around 660 ms (1049 ms vs. 389 ms) faster than the numerical task. As a result, we found asymmetric effects of congruity again: while a large DCE was observed for numerical comparison, no such effect was present in the spatial task. Conditional accuracy plots and cumulative density function plots revealed earliest indications of a DCE in the numerical task after 700 ms, i.e. about 300 ms earlier than in the first two experiments.

2.5 General Discussion of Study 1

This study was designed to provide evidence for a representational link between number and space in terms of distances in either dimension. In three experiments the comparison of numerical distances was influenced by the spatial alignment of the numbers while the numerical information had no impact in a

comparison task of spatial distances. In particular, when the spatial arrangement of the stimuli was (in)congruent with the assumed internal position on the MNL, performance became (worse) better as compared to neutral trials where the middle number was presented midway between the outer numbers. These differences in performance were not restricted to RT but extended to ER in a similar way. Experiment 2 allowed us to rule out a conflict between assigned responses and response codes elicited by attentional shifts as the mechanism underlying the observed DCE. Therefore, we assume that the DCE is evoked by interacting response codes of external and internal spatial intervals. Indeed, the present study underlines the notion of a MNL, but it does not necessarily imply that mental number representations are spatially organized from left-to-right. Instead various spatial configurations are conceivable.

The asymmetry of the observed DCE between tasks might be interpreted in terms of relative speed of information processing for the two dimensions. Since decisions on spatial distance were faster than decisions on numerical distance, the influence of the numerical attribute in the spatial decision was probably weak. In contrast, quickly processed information about spatial distance interfered with the slow numerical decisions. However, other approaches to explain this kind of findings are conceivable: asymmetric interference effects are also found for reasoning about time and space, revealing that people are unable to ignore irrelevant spatial information when making judgments about duration, but not the converse (Casasanto & Boroditsky, 2008). These findings have been interpreted in terms of a parasitic representation of time on spatial representations (Casasanto & Boroditsky, 2008), such that established structures representing space are recruited for new uses like time processing. Our findings suggest that these assumptions may be transferable to the number domain. Number representations might be built on spatial ones, leading us to think about numbers in spatial terms. This assumption applies equally well to the neural level: parietal cortex plays a major role in the processing and perception of spatial information and spatial relations between oneself and the outer world as well as spatial relations between objects in the external world. Recent evidence suggests that parietal cortex is fundamentally and causally involved in numerical cognition (e.g. Hubbard et al., 2005; Knops, Nuerk, Sparing, Foltys, & Willmes, K., 2006). Thus, it has been suggested that a circuitry in parietal cortex shown to be involved in “updating internal representations of space during eye movements” in combination

with the sensitivity of the very same areas to number magnitude change may be perceived as a region that has been “recycled” for accommodating numerical functions and operations (Dehaene & Cohen, 2007, p. 392). In the same vein, it has been suggested that mental arithmetic operations rely on the same neural structures and invoke a subset of operations and mechanisms that are part of the parietal spatial circuitry, such as shifts of spatial attention (Hubbard et al., 2005). Taken together, these assumptions are in line with the claim of a shared representation for numbers, space and time (Walsh, 2003), emphasising a central role of spatial representations. However, further behavioural as well as neuroscience evidence is needed to substantiate this claim further.

3. STUDY 2

SPATIAL REPRESENTATIONS OF NUMBERS IN CHILDREN AND THEIR CONNECTION WITH CALCULATION ABILITIES

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(Co-authored with H. Krinzinger, A. Knops, and K. Willmes)

3.1 Introduction

Only a few studies have addressed the notion of spatial number representations in children. As mentioned above, however, a link between children's numerical and visuo-spatial abilities has been reported in several studies (Ansari et al., 2003; Bachot et al., 2005; De Smedt et al., 2007; Eliez et al., 2001; Simon et al., 2005). Examining second graders (7-8 years; 62 girls and 61 boys), Schweiter et al. (2005) showed that the existence of SNARC effects was marginally correlated with math performance. Interestingly, a marginal positive correlation ($r = .23$) was found for boys, whereas a marginal negative correlation was obtained for girls ($r = -.12$). The authors suggest that gender-specific thinking styles and problem-solving strategies might account for these differences. The assumption of predominantly verbal thinking styles in women and more pronounced visuo-spatial thinking styles in men is based on behavioural studies showing that men perform better on spatial tasks, whereas women outperform men on verbal tasks (e.g. Collins & Kimura, 1997; Halpern, 2000), and on functional imaging studies examining hemispheric lateralization revealing more left lateralized activations during verbal tasks and greater bilateral activity during visuo-spatial tasks for men, as well as greater bilateral activity during verbal tasks and more right lateralized activations in visuo-spatial tasks for women (e.g. Clements et al., 2006).

Taken together, the findings reported above suggest that spatial representations of numbers might have an influence on children's mathematical abilities. Indeed, indications of abnormal number representations in children with combined numerical and visuo-spatial disabilities (Bachot et al., 2005) and joint deficits of number and space processing as observed in children with the chromosome 22q11.2 deletion syndrome (Simon et al., 2005) give reason to assume that spatial number representations are linked with mathematical abilities. But inferring this link from malfunctions is not trivial. As a consequence, supporting evidence deriving from behavioural experiments in typically developing children is important. Schweiter et al. (2005), however, reported only marginal correlations between the size of the SNARC effect and math performance. This might be due to the way spatial number representations and mathematical abilities were assessed.

Mathematical abilities were tested in a wide range of different tasks (as assessed by counting, estimation, transcoding, mental addition, subtraction and multiplication, magnitude comparison, as well as assigning a number to the appropriate position on a visual line). Instead of inspecting correlations between these different variables and the size of the SNARC effect separately, Schweiter et al. (2005) only used an overall score for mathematical abilities. More robust results might have been detectable for more specific abilities like mental addition and subtraction. Moreover, it has been put into question that the SNARC implies a spatial representation of numbers (e.g. Santens & Gervers, 2008).

In the present study the numerical landmark test was used to assess spatial representations of numbers in children at the age of 8-9 years. Apart from inspecting these representations, visuo-spatial and calculation abilities of each child were assessed in order to reveal possible associations between these proficiencies and the DCE. In accordance with the results observed by Schweiter et al. (2005), possible differences between boys and girls were also explored.

3.2 Method

3.2.1 *Participants*

The participants were 118 (66 female) German children from grade 3 (mean age 8.5, range 8-9 years) recruited from five primary schools in Aachen (Germany). All participants had normal or corrected to normal vision. Written and informed consent was obtained from all parents and teachers involved.

3.2.2 *Tasks*

A numerical landmark test was used to look for spatial representations of numbers in children. Visuo-spatial abilities were assessed by the Beery-Buktenica Developmental Test of Visual-Motor Integration (VMI; Beery, 1997). Calculation abilities were examined by addition and subtraction problems. While the numerical landmark test was carried out individually, visuo-spatial as well as calculation abilities were assessed by paper-pencil tasks in groups of about 20 children.

In the numerical landmark test children had to decide which one of the two numerical distances in a number triplet was numerically larger. The stimulus set

consisted of 16 two-digit number triplets. Four numerical distance-pairs (ND, i.e. numerical distance between the middle number and the outer numbers) were used. These were determined as percentages of the numerical distance between the two outer numbers, which was always 35, resulting in ND 20/80: 7/28; ND 40/60: 14/21; ND 60/40: 21/14; and ND 80/20: 28/7. For each of the four numerical distance-pairs, four different number triplets were employed, resulting in a total of 16 different triplets. These triplets were matched for problem size (sum of all three numbers), parity, and number of decade crossings. None of the number triplets was part of a multiplication table or included decade numbers.

Beside the four numerical distance-pairs, four spatial distance-pairs (SD) were used, which were calculated as percentages of the spatial distance between the two outer numbers, which was always 7cm (visual angle of 6.7°), resulting in SD 20/80: 1.4 cm/5.6 cm; SD 40/60: 2.8 cm/4.2 cm; SD 60/40: 4.2 cm/2.8 cm; and SD 80/20: 5.6 cm/1.4 cm (see Figure 1). Combining all of the 16 number triplets with these spatial variations resulted in 64 different stimuli, of which 32 were congruent and 32 were incongruent. Additionally, 32 neutral stimuli were included. They consisted of the 16 number triplets with the spatial distance-pair (SD 50/50: 3.5 cm/3.5 cm) used twice. The two-digit numbers had a visual angle of 0.5° in height (5 mm) and of 0.7° in width (7 mm) from a viewing distance of about 60 cm.

Children had to indicate the side where the numerical distance was larger by answering with the left index finger when it was larger on the left side and by using the right index finger when it was larger on the right side. Responses were given via the left and right CTRL-buttons of a notebook keyboard. RT and ER were recorded and the instruction stressed both speed and accuracy. The trials were pseudo-randomized so that there were no consecutive identical number triplets and numerical (or spatial) distance-pairs were not identical on more than two consecutive trials. Moreover, the position of the two-digit numbers in consecutive trials was horizontally shifted on the screen (from 0.4 mm to 6 mm, visual angles of 0.04° to 0.6°) to make sure that consecutive number triplets never appeared at exactly the same position.

The experiment was preceded by 10 warm-up trials to familiarize participants with the task (data not recorded) and controlled by a notebook with Presentation[®] software (Neurobehavioral Systems, Inc.). The targets were white digits presented on a 17" colour monitor (1280 by 1024 pixel) against a black background. A trial started

with the presentation of a fixation cross for 500 ms. After the fixation cross had vanished the target appeared until the response, but only up to a maximum duration of 4000 ms, and was followed by a black screen for 500 ms. Carrying out the number landmark test took about five minutes.

The Beery-Buktenica Developmental Test of Visual–Motor Integration (VMI; Beery, 1997) contains a developmental sequence of 27 geometric forms (with increasing grades of difficulty) to be copied on paper. Only forms 13 to 27 were used. We refer to this task as the “VMI-copying task”. In the supplementary Visual Perception test of the VMI, the forms 14 to 27 were presented. For each form, an identical form had to be chosen among 5, 6, or 7 others that looked nearly but not exactly the same, by marking the respective form. We refer to this task as the “VMI-visual-discrimination task”. Because of time constraints, only the more complex geometric forms were selected. Carrying out the visuo-spatial tasks took about ten minutes.

The addition and subtraction problems consisted of 9 blocks of 10 arithmetic problems; 5 blocks were addition problems and 4 blocks subtraction problems. The addition problems were divided in two blocks, in which a single-digit number had to be added to a two-digit number with only one of these blocks requiring carrying. Moreover, three blocks contained addition problems, in which two two-digit numbers had to be added. In only one of these latter blocks, one of the addends was a decade number. Among the remaining two blocks without decade numbers, again, only one block required carrying. The subtraction problems were structured in a similar way: there were two blocks, in which a single-digit number had to be subtracted from a two-digit number and two blocks, which required subtraction of a two-digit number from another two-digit number. In both cases one block required borrowing, while the other one did not. Children were given 30 seconds to work on a single block.

3.3 Results

To evaluate data from administration of the numerical landmark test, repeated measures analyses of variance (ANOVAs) and post-hoc tests for further investigations were conducted separately for RT and ER. ER was arcsine-transformed ($2\arcsin\sqrt{ER}$). The Huynh-Feldt epsilon (Huynh & Feldt, 1976) was

computed to correct the degrees of freedom of the F-statistics in case of significant ($\alpha = 10\%$) non-sphericity. Only correct responses were used for calculating mean RT. Trials in which no response occurred were classified as errors. Responses below 200 ms were excluded from further analysis, as well as responses outside an interval of ± 3 standard deviations around the individual mean. Trimming resulted in 4.0% of response exclusions. Nine participants were excluded from further analyses because of only incorrect answers in one of the different conditions.

Pearson correlation coefficients were employed to look for possible relations between the size of the congruity effect in the landmark paradigm and visuo-spatial as well as calculation abilities. Another nine children had to be excluded from the analysis, because they did not take part in the group testing, in which visuo-spatial and calculation abilities had been assessed. All effects were tested using a significance level of $\alpha = 5\%$.

3.3.1 Numerical landmark test

Reaction time

An ANOVA including the within-subject factors congruity (congruent, neutral, incongruent), distance (small [ND 40/60 or ND 60/40] vs. large [ND 20/80 or ND 80/20]), and the between-subject factor sex revealed significant main effects for distance ($F(1, 99) = 26.80, p < .001$) and for congruity ($F(2, 198) = 4.25, p < .05$). The main effect for distance was characterized by faster RT for large compared to small distances (small: 2474 ms, large: 2366 ms), while the main effect for congruity showed fastest mean RT for neutral and slowest mean RT for incongruent trials (see Table 2). Additionally, a significant interaction between congruity and distance was found ($F(2, 196) = 4.44, p < .05, \epsilon = .957$).

Separate ANOVAs for the two different distances revealed that the main effect for congruity was only found for large distances ($F(2, 198) = 6.76, p = .001$): RT was fastest for congruent and slowest for incongruent trials. As indicated by post-hoc paired-sample *t* tests, the only significant difference was found between the incongruent and the congruent condition ($p < .01$, see Table 2). To illustrate the distribution of the DCE over the whole range of latencies, plots with the cumulative density function for deciles (Ridderinkhof, 2002) are provided in Figure 8. According to visual inspection of the graphs, the congruity effect mainly arose between the

fourth and the ninth response deciles (mean RT between 2100–3200 ms). No other interaction reached significance.

Error rate

On the basis of ER, significant main effects of distance (small: 44.0%, large: 24.1%; $F(1, 99) = 384.42, p < .001$) and of congruity ($F(2, 198) = 22.17, p < .001$, $\epsilon = .959$) were found. ER was relatively high, particularly for triplets with small distances. The main effect for congruity was characterized by the smallest mean ER for congruent and the highest one for incongruent trials. As indicated by post-hoc paired-sample t tests, all conditions differed significantly from each other also after correction for multiple testing (incongruent vs. congruent: $p < .001$, incongruent vs. neutral: $p < .01$, neutral vs. congruent $p < .01$; see Table 2), reflecting a DCE.

Table 2

Mean reaction times for correct responses in ms and percentage of errors in the numerical landmark test averaged over small and large distances and separately for each distance as a function of the factor congruity (congruent vs. neutral vs. incongruent) with standard deviations in parentheses.

		Congruent	Neutral	Incongruent
Small and large distances	RT in ms	2388 (341)	2382 (349)	2449 (359)
	ER in %	30 (11)	34 (11)	38 (11)
Small distances	RT in ms	2493 (382)	2423 (397)	2505 (472)
	ER in %	40 (13)	44 (13)	49 (14)
Large distances	RT in ms	2316 (366)	2361 (373)	2421 (349)
	ER in %	20 (13)	25 (13)	27 (15)

As can be seen from the conditional accuracy functions in Figure 8 (Ridderinkhof, 2002), the DCE based on ER mainly arose between the first and the sixth response accuracy deciles (mean RT between 1600–2600 ms). There was no trade-off between mean RT and ER ($r = -.110$; $p = .278$ two-sided). Item-specific performance for each of the 16 different triplets is reported in the Appendix A.

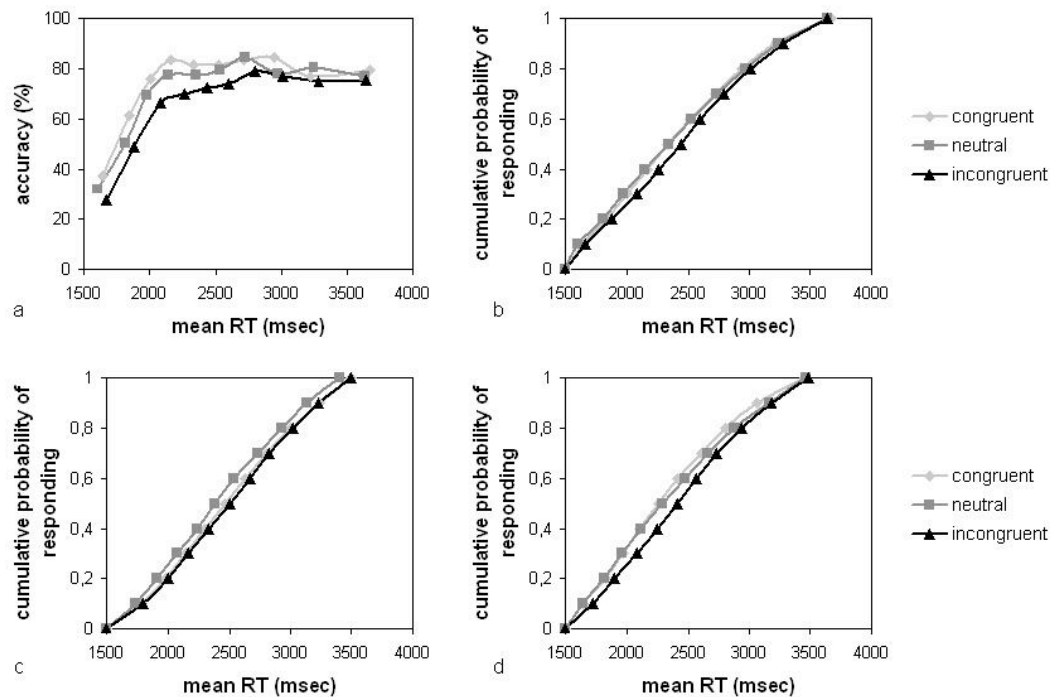


Figure 8. Conditional accuracy functions (a) and cumulative density functions (b) averaged over small and large distances as a function of the factor congruity (congruent vs. neutral vs. incongruent), as well as cumulative density functions separately for small (c) and large (d) distances. Cumulative density functions were approximated by plotting separately for congruent, neutral, and incongruent conditions the cumulative probability of responding as a function of mean RT (only correct responses) for each of the ten response speed deciles. Conditional accuracy functions were approximated by plotting separately for congruent, neutral, and incongruent conditions accuracy as a function of mean RT (only correct responses) for each of ten response accuracy deciles.

Associations between the DCE and visuo-spatial as well as calculation abilities

Pearson correlation coefficients were computed to look for possible associations between the size of the DCE and visuo-spatial as well as calculation abilities. To assess the DCE, mean difference values (incongruent - congruent)¹ were

¹ Instead of using difference values to assess the DCE, the raw average RT and error data for the congruent as well as for the incongruent condition were entered in a supplementary correlation

computed for each participant separately for RT and for ER, with positive values indexing the DCE. Total scores, ranging from 0 to 15 in the VMI-copying task, from 0 to 14 in the VMI-visual-discrimination task, and from 0 to 90 for the addition and subtraction problems, were used to estimate visuo-spatial and calculation abilities, higher raw score totals pointing to better abilities.

Intercorrelations of the different variables are shown in Table 3. The DCE based on RT was significantly correlated with performance in the VMI-copying task and this performance in the VMI-copying task was marginally correlated with calculation abilities ($p = .078$ two-sided). As expected, significant correlations were found between the DCE based on RT and the DCE based on ER, as well as for performance in the VMI-copying task and performance in the VMI-visual-discrimination task. No other significant correlations were present.

Inspired by the findings of Schweiter et al. (2005), who reported marginal correlations between the size of the SNARC effect and math performance - positive for boys and negative for girls - a gender-specific analysis was carried out as well. For boys, a significant positive correlation between calculation abilities and the DCE based on RT (and based on ER; see Figure 9) and a significant positive correlation between calculation abilities and performance in the VMI-copying task as well as in the VMI-visual-discrimination task were found. Significant correlations were also obtained between performance in the VMI-copying task and performance in the VMI-visual-discrimination task as well as for the DCE based on RT and the DCE based on ER. For girls, on the other hand, a marginal negative correlation ($p = .092$ two-sided) between calculation abilities and the DCE based on ER was obtained (see Figure 9). Performance in the VMI-copying task was significantly correlated with the DCE based on ER, but calculation abilities did not correlate with performance in the visuo-spatial tests. In addition, performance in the VMI-copying task and performance in the VMI-visual-discrimination task correlated significantly, but values for the DCE based on RT and the DCE based on ER correlated only marginally ($p = .095$ two-sided; see Table 3).

Table 3

Pearson correlation coefficients between calculation abilities, performance in the VMI-copying task, performance in the VMI-visual-discrimination task, DCE based on RT, and DCE based on ER for all participants and separately for girls and boys.

		VMI- copy task	VMI- discrimination task	DCE based on RT	DCE based on ER
Calculation abilities	overall:	0.18	0.11	0.14	0.10
	girls:	0.07	-0.01	-0.01	-0.22
	boys:	0.33*	0.35*	0.35*	0.32*
VMI- copy task	overall:		0.54**	0.20*	0.16
	girls:	-	0.50**	0.19	0.34*
	boys:		0.57**	0.21	0.01
VMI- discrimination task	overall:			0.02	-0.01
	girls:		-	0.04	0.19
	boys:			-0.01	-0.17
Congruity effect RT	overall:				0.29**
	girls:			-	0.22
	boys:				0.40**

* $p < 0.05$, ** $p < 0.01$ (two-sided); $n = 100$ (58 girls, 42 boys)

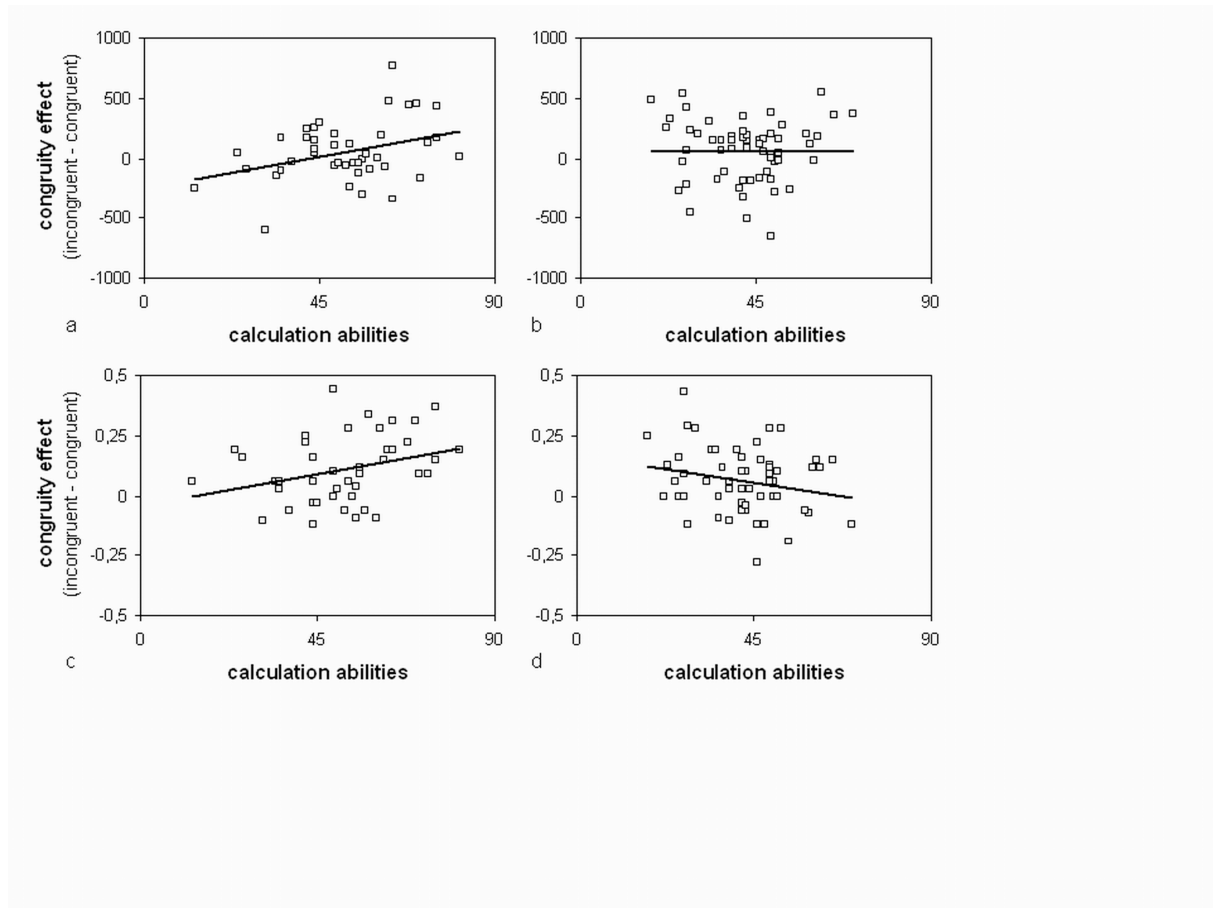


Figure 9. Correlation between calculation abilities (raw score totals, theoretical range: 0-90) and the DCE (incongruent - congruent) based on RT separately for boys (a) and girls (b), as well as the correlation between calculation abilities and the DCE based on ER separately for boys (c) and girls (d).

These findings indicate that connections between the DCE and calculation as well as visuo-spatial abilities seem to be differently marked for girls and boys. The direct comparison of both correlation coefficients (see Millsap et al., 1990) yielded significant differences for the correlation between calculation abilities and the DCE based on ER ($p < .01$ two-sided), while marginal differences were found for the correlations between calculation abilities and the DCE based on RT ($p = .077$ two-sided) as well as for the correlation between calculation abilities and performance in the VMI-visual-discrimination task ($p = .074$ two-sided). In addition, calculation abilities, performance in the VMI-copying task, performance in the VMI-visual-discrimination task, DCE based on RT, DCE based on ER, overall RT and ER of the numerical landmark test were compared between girls and boys (see Table 4): a

significant difference was only found for calculation abilities, showing that boys performed better than girls on average.

Table 4

Comparison between girls and boys (two-sample t tests) with respect to calculation abilities, performance in the VMI-copying task, performance in the VMI-visual-discrimination task, DCE based on RT, DCE based on ER, overall RT (only correct responses) and ER of the numerical landmark test with standard errors of the mean and standard deviations in parentheses.

	Sex	Mean	Standard error of mean
Calculation abilities*	girls	43 (12)	1.52
(theoretical range: 0-90)	boys	52 (15)	2.30
VMI-copy task	girls	11 (2)	0.23
(theoretical range: 0-15)	boys	10 (2)	0.35
VMI-discrimination task	girls	11 (2)	0.25
(theoretical range: 0-14)	boys	10 (2)	0.32
DCE based on RT	girls	66 (256)	33.60
(ms)	boys	54 (249)	38.37
Overall RT	girls	2432 (314)	41.24
(ms)	boys	2361 (332)	51.16
DCE based on ER	girls	6 (13)	1.74
(%)	boys	11 (14)	2.16
Overall ER	girls	33 (9)	1.16
(%)	boys	35 (8)	1.17

* $p < 0.05$ (two-sided) Bonferroni corrected for multiple comparisons; $n = 100$ (58 girls, 42 boys)

3.4 Discussion

In the present study, a DCE was found for children at the age of 8-9 years: lower ER for congruent and higher ER for incongruent compared to the neutral trials. Based on RT fastest responses were found for the neutral condition and not for the congruent one. However, separate analyses for the two different distance levels

(small or large) revealed fastest RT for the congruent condition and slowest RT for the incongruent condition, but only for large distances. The ambiguous results for triplets including small distances may be due to the fact that it was very difficult to work on these triplets for a large proportion of the participating children: mean error rate was close to chance level (44%, ranging from 23-67%).

Conditional accuracy plots and cumulative density function plots (Ridderinkhof, 2002) demonstrated that the DCE based on ER mainly arose between the first and the sixth response accuracy deciles (mean RT between 1600–2600 ms) and the DCE based on RT was primarily present between the fourth and the ninth response deciles (mean RT between 2100–3200 ms). In terms of a relative speed account (see Schwarz & Ischebeck, 2003), the degree of cross-dimensional influence depends on the relative time necessary for processing information of the dimensions involved. It is plausible to assume that spatial distance information was available at a point in time where numerical distances were still analysed. Therefore the reported time-frames might indicate that the difference between the spatial distances was processed and still present between 1600 ms and 3200 ms after stimulus onset, exerting a strong influence during this time-interval.

Larger ER as well as slower RT were observed for small compared to large distances, representing a classical effect of distance (e.g. Moyer & Landauer, 1967 for single-digit numbers; Dehaene, 1989; Nuerk, Weger, & Willmes, 2001 for two-digit numbers). This finding underlines that the children actually followed the instructions and compared the numerical distances within the different number triplets.

Results of a gender-specific correlation analysis revealed a (weak) positive connection between the size of the DCE (based on RT and ER) and performance in the calculation tasks for boys and a marginal negative connection for girls (only for the ER)². These results are in line with the findings by Schweiter et al. (2005), showing a marginal positive correlation between the size of the SNARC effect and math performance for boys and a marginal negative correlation for girls. According to the authors gender-specific thinking styles and problem-solving strategies might account for these differences. Indeed, this account may explain the reported findings: large proportions of girls and boys at the age of 8-9 years seem to represent numbers spatially, as evidenced by the DCE, which was equally pronounced for girls

² The non-uniform results for the DCE based on RT might be due to the fact that the DCE based on RT was not as stable as the DCE based on ER.

and boys (see Table 4). But depending on the preferred thinking style, this kind of representation might have a supportive or detrimental influence on calculation skills. As a consequence, for boys, who may prefer visuo-spatial thinking styles, a spatial representation of numbers could be helpful when being confronted with addition or subtraction problems, whereas for girls preferring verbal thinking styles it might be even obstructive. This could in turn account for the gender difference found for calculation abilities: in agreement with the study by Schweiter and coworkers and other studies examining mathematical abilities (e.g. Geary, 1996), we found that boys performed better than girls on average when asked to solve addition and subtraction problems involving two-digit numbers.

In the visuo-spatial tasks no gender difference was found, possibly due to the specific task used. It is true that the most consistent findings of gender differences come from research on visuo-spatial tasks, but especially from those involving mental rotation (Linn & Petersen, 1985), which was not looked at in this study. Interestingly, we found that performance in the visuo-spatial tasks was positively correlated with calculation abilities only for boys. This might underline the assumption that boys rely more on visuo-spatial strategies than girls when asked to solve addition or subtraction problems. Only for girls on the other hand there was a positive correlation between performance in the VMI-copying task and the DCE based on ER. This might reflect that those girls showing a DCE might have better visuo-spatial abilities than the others.

Since only correlations were reported here, strong conclusions can not be drawn: connections between spatial representations of numerical magnitude and calculation as well as visuo-spatial abilities in children at the age of 8-9 years seem to be differently marked for girls and boys. As mentioned above, a possible explanation for these findings may be based on the notion of different thinking styles. Further evidence is needed to substantiate this claim. If valid, it may provide important implications for remediation programs for dyscalculic children and adults.

4. STUDY 3

NUMBERS AND SPACE –

EVIDENCE FOR A LINK FROM HIGH-RESOLUTION FMRI

Submitted for publication.

(Co-authored with A. Knops, J.W. Koten, and K. Willmes)

4.1 Introduction

As has been reported above, overlapping neural structures might be responsible for inducing numerical-spatial interactions (Dehaene & Cohen, 2007; Hubbard et al., 2005; Walsh, 2003). In humans, however, this overlap remains only tentative, given that brain regions have been defined only on the basis of fMRI studies using spatial resolutions of no less than $3 \times 3 \times 3 \text{ mm}^3$. Moreover, the idea of neural overlap has to be explored in a within-subject design given the differences in individual anatomy. To address these issues empirically, an fMRI study was conducted to identify human brain areas being responsible for subtraction, visual motion processing and saccades. In addition, the neural correlate of the DCE was assessed. More specifically, no study so far has shown the neural correlate of the putative association between numerical magnitude and space, i.e. that the mental representation of number is conceptualized as a mental number line. Here we sought to provide neurofunctional evidence for this widely accepted assumption. To increase the anatomical resolution we used functional imaging sequences with a relatively small voxel size ($2 \times 2 \times 2 \text{ mm}^3$) that allows for a more fine-grained functional parcellation of different areas as compared to previous studies.

4.2 Method

4.2.1 Participants

Eighteen (9 female) right-handed participants (mean age 26.1, range 19-32 years) were tested in this study, which was approved by the local Ethics Committee of the Medical Faculty, RWTH Aachen University. Due to head movement artefacts three participants (1 female, 2 male) had to be rejected. All participants had normal or corrected to normal vision.

4.2.2 Tasks

Cerebral activations were studied for four different tasks: the numerical landmark test, a subtraction task, a visual motion processing task, and a saccades

task. Participants were introduced to all of the tasks before fMRI scanning. The numerical landmark test was conducted in an event-related design and divided in two identical blocks of 120 trials each. The other three tasks were administered in a block design. Each of these latter three tasks was compared to a specific control task matched for stimulus characteristics. During an fMRI scanning sequence, 8 blocks (12 trials each) were presented with an alternation of primary task and control task blocks (4 blocks each). Breaks of 20 seconds separated the different blocks. Each participant started with the numerical landmark test, while the sequence of the remaining three tasks was counterbalanced across participants. Stimuli were presented via a head-mounted video display designed to meet MR requirements. The whole experimental procedure lasted approximately 90 min and was controlled by Presentation[®] software (Neurobehavioral Systems, Inc.).

Numerical landmark test

In the numerical landmark test participants had to decide which one of the two numerical distances in a number triplet was numerically smaller. The stimulus set consisted of 16 two-digit number triplets spatially arranged in a horizontal fashion on the screen at two varying spatial intervals between the middle number and the outer two numerals (see Figure 10). The constituting numerals of a triplet were always arranged in numerically ascending order from left to right. Numerical and spatial distances were manipulated independently. As a result, numerical and spatial intervals could be congruent or incongruent. In neutral triplets, spatial intervals were identical. The stimulus set was identical to the one used in *Study 2* but presented twice. The participants had to indicate the side where the numerical distance was smaller by pressing a response button with the left index finger when it was smaller on the left side and by using the right index finger when it was smaller on the right side. RT and ER were recorded and the instruction stressed both speed and accuracy. Digits were presented in white colour against an otherwise black background and had a visual angle of 0.7° in height (10 mm) and of 0.5° in width (7 mm). The two blocks of 120 trials each were separated by a break of one minute. Each block included 24 null-events, in which a black screen was presented. A trial started with the presentation of a fixation cross for 500 ms. After the fixation cross had vanished the target appeared until the response, but only for a maximum

duration of 3000 ms, followed by a black screen for a varying time interval (500, 1000, 1500, 2500, 3500, or 6000 ms with 2500 ms on average).

Subtraction task

In the subtraction task, stimuli were white Arabic digits from 2 to 9 with a visual angle of 0.7° in height (10 mm) and of 0.5° in width (7 mm) presented at fixation and against a black background (see Figure 10). Each trial started with the presentation of a digit appearing for 150 ms, which was then replaced by a fixation cross. Participants were instructed to subtract the respective number from 11 and to name the result mentally within 3000 ms. In the control naming task, stimuli were uppercase letters between B and J, excluding I because of its similarity to the digit “1”. Participants were asked to name each letter mentally (see Simon et al., 2002 for a similar procedure).

Visual motion processing task

For visual stimulation we used flow-field stimuli (see Figure 10) consisting of 160 randomly distributed white dots (dot size ranging from 0.1° to 0.5° of visual angle) either expanding (two blocks) or contracting (two blocks) coherently (see Bremmer, Ilg, Thiele, Distler, & Hoffmann, 1997 for a similar procedure). Each trial consisted of the presentation of a random dot pattern for 3000 ms moving in steps of 100 ms. Dots moving out of the visual field were replaced. Participants were instructed to fixate the centre of the screen, which was marked by a white square (0.6° of visual angle). As a control, participants fixated the central square, while being confronted with random dot patterns, which remained stationary for 3000 ms.

Saccades task

In the saccades task participants were shown eight boxes (each with a visual angle of 1.2° in width and height) arranged in a circle at 6° eccentricity from a similar box positioned at the centre of the screen (see Figure 10). Each trial started with the presentation of a white square appearing within a randomly chosen box for 150 ms, which was replaced by a fixation cross centred in that box. The participants were asked to move their eyes toward this box and fixate it for 2000 ms until the next trial

appeared. In the control fixation task, participants had to fixate a cross in the central box, while white squares appeared in the surrounding boxes following the same order as in the primary task (see Simon et al., 2002 for a similar procedure).

4.2.3 Imaging protocol

Functional images were acquired on a 3T Philips Gyroscan NT with a SENSE head coil. Transversal multislice T2*-weighted images were obtained with a gradient echo planar imaging sequence (TE = 30 ms; TR = 2 s; 80×80 matrix; flip angle = 90°; 24 slices, 2×2mm² in-plane resolution; slice thickness 2 mm) covering most of the frontal, of the parietal and of the occipital lobe (see Appendix C). During the numerical landmark test 780 volumes were acquired, while in each of the other three tasks 250 volumes were recorded. Each part of a session started with 5 dummy scans to allow tissue to reach steady state magnetization. These were not recorded for data analysis. A high-resolution T1-weighted three-dimensional anatomical image was also acquired (TE = 4.59 ms; 256×256 matrix; voxel dimensions = 1×1×1 mm³).

4.2.4 Data analysis

Analyses of variance (ANOVAs) and Bonferroni corrected post-hoc *t* tests for further investigations were conducted separately for RT and ER. ER was arcsine-transformed ($2\arcsin\sqrt{ER}$). Only correct responses were used for calculating mean RT. Trials in which no response occurred were classified as errors. Responses below 200 ms were excluded from further analysis, as well as responses outside an interval of ± 3 standard deviations around the individual mean. Trimming resulted in 0.7% of response exclusions.

Neuroimaging data were preprocessed and analysed using BrainVoyager QX 1.9 software (Brain Innovation, Maastricht, The Netherlands; Goebel, Esposito, & Formisano, 2006). Preprocessing was done separately for each of the four parts of a session and included slice scan time correction (using cubic spline interpolation), temporal high-pass filtering, and 3D-motion correction. Estimated translation and rotation parameters never exceeded 2 mm. Functional datasets were co-registered to the Talairach-transformed (Talairach & Tournoux, 1988) anatomical image.

All individual brains were segmented at the gray/white matter boundary using a semiautomatic procedure based on intensity values (ITK-SNAP; Yushkevich et al.,

2006). Furthermore, cortical surfaces were reconstructed, inflated, and flattened with BrainVoyager QX 1.9 software. A high-resolution cortical alignment method using curvature information reflecting the gyral/sulcal folding pattern was used to improve correspondence across brains beyond Talairach space matching. Using unsmoothed data, this kind of cortex-based analysis has been shown to reveal spatially more confined group clusters of activation (Goebel et al., 2006).

Random-effects analyses were performed on the group data ($n = 15$) level. Statistical maps were reported using a liberal threshold of $t = 1.64$ for the contrast of incongruent minus congruent stimuli in the numerical landmark test. Note that these conditions differed only with respect to the spatial layout of the number triplets, which was not task-relevant. For the other three tasks, which were accomplished in a block design, the same threshold of $t = 1.64$ was used whereas cluster size limits for multiple probability thresholds were estimated using random fields theory and validated with Monte Carlo simulation (see Hagler, Saygin, & Sereno, 2006)

4.3 Results

At the behavioural level the comparison of numerical distances was influenced by the spatial alignment of the numbers in the numerical landmark test (see Figure 10 for a schematic depiction). In particular, when the spatial distances between the respective numbers were (in)congruent with the numerical ones, performance became (worse) better as compared to neutral trials where the middle number was presented midway between the outer numbers. These differences in performance were not restricted to RT (congruent: 1457 ms [standard deviations = 270 ms], neutral: 1515 ms [254 ms], incongruent: 1585 ms [288 ms], $F(2, 28) = 35.75$, $p < .001$) but extended to ER in a similar way (congruent: 9.4% [5.8%], neutral: 12.9% [7.7%], incongruent: 19.8% [6.5], $F(2, 28) = 28.30$, $p < .001$). In 14 out of 15 participants a congruity effect on both of these parameters was detected (see Figure 15).

Neuroimaging results mainly revealed networks comprising parietal and frontal areas in each of the different tasks. First, patterns of activations observed in each task relative to the respective control condition will be described (see Figure 10; Table 5). In the following, the focus will be on overlapping activations of the neural

correlate of the congruity effect found in the numerical landmark test with the other different tasks.

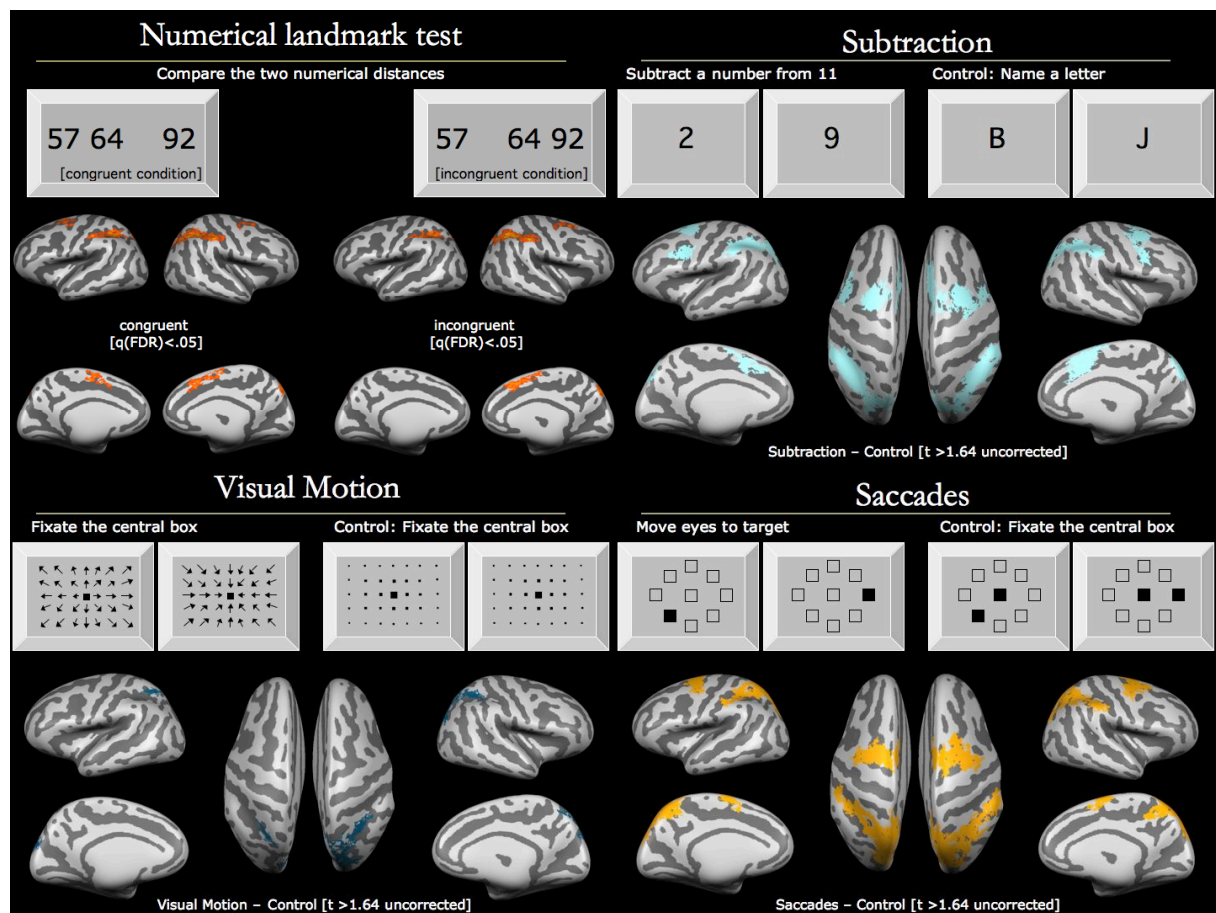


Figure 10. Schematic depiction of the four tasks and corresponding brain activations. For the numerical landmark test activity during the congruent and the incongruent condition (each contrasted with the rest condition) is presented. For the other three tasks primary and control tasks were contrasted. Resulting activations are shown on left (lateral/medial), top, and right (lateral/medial) views of cortically aligned hemispheres. The cortical surfaces were defined individually at the gray-white matter boundary and have been partially inflated. Sulci are indicated in dark gray and gyri in light gray. Depictions of the tasks were black/white inverted for better visibility.

Table 5

Areas activated during each of the four tasks relative to their respective controls.

Task	Anatomical region	Talairach coordinates (x,y,z)			t values (peaks)
Numerical landmark test (incongruent - congruent)	Inferior parietal lobule	-47	-43	40	3.82
		41	-43	39	3.80
	Supramarginal gyrus	-41	-42	37	2.35
	Precuneus	-19	-69	44	4.14
		9	-56	41	3.72
	Middle frontal gyrus	37	2	38	2.16
	Superior frontal gyrus	22	8	52	4.73
	Medial frontal gyrus	8	18	44	3.26
	Cingulate gyrus	-3	-4	33	3.79
		9	17	44	4.05
	Precentral gyrus	37	1	35	2.80
Calculation	Inferior parietal lobule	-30	-45	38	8.11
		41	-45	39	9.44
	Superior parietal lobule	-29	-47	38	6.05
		31	-50	40	3.93
	Angular gyrus	-34	-59	37	5.08
		35	-59	38	5.42
	Supramarginal gyrus	-40	-44	37	6.97
		55	-37	37	2.84
	Precuneus	-30	-45	40	7.25
		12	-71	39	10.74
	Inferior frontal gyrus	-37	4	29	2.59
		39	5	24	2.52
	Middle frontal gyrus	-22	-3	49	5.34
		34	-1	54	6.04
	Superior frontal gyrus	-18	5	60	3.45
		10	20	50	5.11
	Medial frontal gyrus	-6	-6	59	5.88
		10	20	47	5.77
	Cingulate Gyrus	-9	7	42	4.36
		11	7	36	5.66
	Precentral gyrus	-35	0	32	3.89
		44	-1	30	3.73
	Postcentral gyrus	53	-29	38	3.70
	Cuneus	-27	-74	28	3.19
		8	-70	34	3.62
	Superior occipital gyrus	-27	-75	26	2.91
		31	-70	26	3.78
	Middle occipital gyrus	31	-74	25	2.65
Visual motion	Inferior parietal lobule	-31	-45	43	1.72
		33	-46	39	4.11
	Superior parietal lobule	-27	-57	47	3.33
		18	-65	51	4.38
	Precuneus	-23	-60	50	4.30
		19	-73	41	5.80
	Cuneus	-11	-84	29	3.15
		18	-78	33	4.48
	Superior occipital gyrus	32	-73	25	2.93
	Middle occipital gyrus	-14	-89	18	1.91
Saccades		30	-75	25	2.58
	Inferior parietal lobule	-33	-41	43	5.27
		52	-31	39	4.71
	Superior parietal lobule	-27	-52	42	4.94

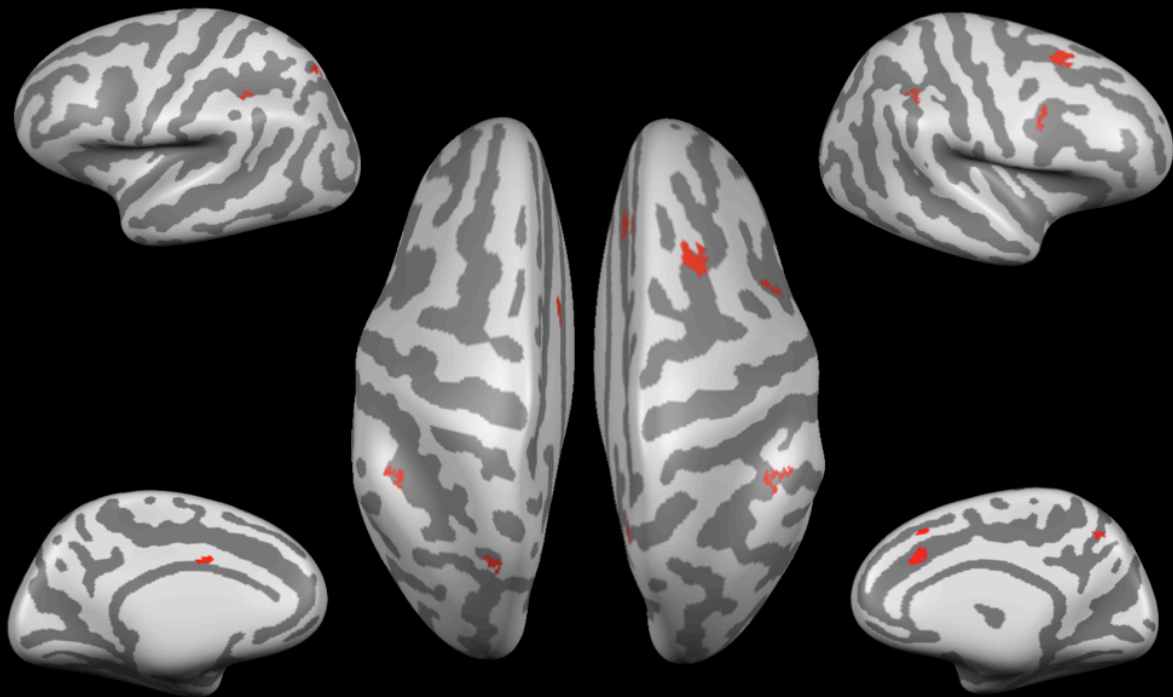
	18	-62	54	6.01
Angular gyrus	-30	-55	38	2.22
	36	-57	39	3.21
Supramarginal gyrus	-38	-41	37	3.35
	56	-37	36	2.33
Precuneus	-17	-72	43	8.46
	15	-73	39	6.92
Middle frontal gyrus	-27	-8	47	5.27
	29	-11	46	6.49
Superior frontal gyrus	-13	-14	65	4.90
	9	-5	64	4.96
Medial frontal gyrus	-6	-8	63	6.25
	11	-10	65	4.26
Cingulate Gyrus	-7	-1	45	4.15
	11	-42	41	4.75
Precentral gyrus	-24	-12	46	4.39
	33	-12	50	5.90
Postcentral gyrus	-43	-29	37	3.16
	50	-29	38	2.81
Cuneus	-19	-72	35	3.97
	16	-82	30	2.92
Middle occipital gyrus	-17	85	17	1.83
	29	-76	24	2.39

4.3.1 Numerical landmark test

The activation pattern during the numerical landmark test was very similar to the one observed in the subtraction task (see Figure 10). In order to assess the neural correlates of the congruity effect, the congruent condition was subtracted from the incongruent one. This revealed bilateral activations with more clusters of activation in the right hemisphere. In both hemispheres clusters in the inferior parietal lobule, the precuneus, and the cingulate gyrus were observed. Additional activations were found in the superior/middle frontal gyrus, in the medial frontal gyrus, and in the precentral gyrus extending into the middle frontal gyrus, but only in the right hemisphere. Plotting the fitted BOLD response over time for the activation spots in the left and right inferior parietal lobule and the precuneus mirrored the behavioural congruity effect at the neural level (see Figure 11).

Congruity Effect

incongruent – congruent [$t > 1.64$ uncorrected]



congruent neutral incongruent

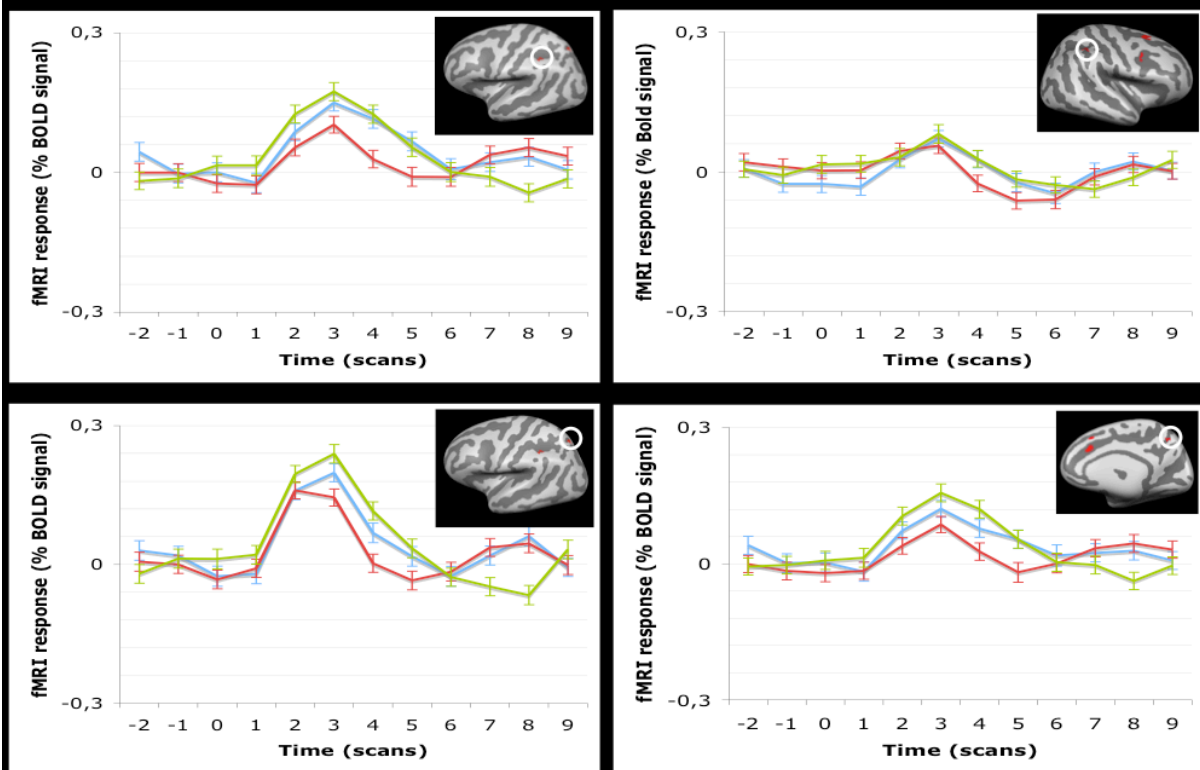


Figure 11. The neural correlate of the congruity effect presented on left (lateral/medial), top, and right (lateral/medial) views of cortically aligned hemispheres: in the bottom part of the figure average time courses from selected regions of interest in the parietal cortex are shown as a function of congruity (congruent, neutral, incongruent). Stimulus onset was at time point zero.

Spots in the inferior parietal lobule correspond with previous localizations of anterior intraparietal areas (AIP) and coordinates of neurons in the precuneus show agreement with areas IPTO (area around the junction of the intraparietal and transverse occipital sulci, see Culham and Valyear, 2006) or PSPL (posterior superior parietal lobule, see Dehaene et al., 2003), which are assumed to play a central role in eye movements and attention orienting (see Table 6).

Table 6

Talairach coordinates of anterior and posterior parietal areas (AIP = anterior intraparietal, IPTO = area around the junction of the intraparietal and transverse occipital sulci, PSPL = posterior superior parietal lobule) derived from neuroimaging studies in humans and from the current study (¹neural correlates of the congruity effect in inferior parietal and supramarginal areas; ²neural correlates of the congruity effect in the precuneus). Coordinates from Schluppeck et al., Silver et al., and Hagler et al. have been averaged across right and left hemispheres for two or three adjacent spots. Coordinates from Dehaene et al. represent average data from different studies.

	Left hemisphere (x,y,z)			Right hemisphere (x,y,z)		
AIP						
Binkofski et al., 1999	-40	-40	40	40	-40	-44
Grefkes et al., 2002	-40	-42	36			
Mecklinger et al., 2002	-44	-46	42			
Tanabe et al., 2005				38	-40	44
Congruity effect¹	-47	-43	40	41	-43	39
	-41	-42	37			
IPTO						
Koyama et al., 2004	-20	-63	49	19	-63	49
Schluppeck et al., 2005	-21	-76	42	21	-76	42
	-18	-71	52	18	-71	52
Silver et al., 2005	-23	-76	39	23	-76	39
	-19	-75	48	19	-75	48
Hagler et al., 2007	-20	-69	43	20	-69	43
	-19	-64	51	19	-64	51
	-23	-57	51	23	-57	51
PSPL						
Dehaene et al., 2003	-22	-68	56	15	-63	56
Congruity effect²	-19	-69	44	9	-56	41

4.3.2 Subtraction task

Contrasting calculation against letter naming, we observed bilateral activation clusters that included frontal areas (superior/inferior/middle/medial frontal gyrus and pre-/postcentral gyrus), parietal cortex (superior/inferior parietal lobule, supramarginal/angular gyrus and precuneus), occipital areas (superior/middle occipital gyrus and cuneus/precuneus) and the cingulate gyrus (see Figure 10). These findings mainly parallel the ones reported by Simon et al. (2002) and many others and can readily be summarized as activations in a fronto-parietal network.

4.3.3 Visual motion processing task

Visual motion processing increased neural activity bilaterally with more clusters of activation in the right hemisphere. Activations in the right hemisphere were observed in occipital (superior/middle occipital gyrus and cuneus/precuneus) and parietal areas (superior/inferior parietal lobule, and precuneus). Similar but less activation was found in the left hemisphere (see Figure 10). These observations are in line with previous studies using similar tasks (e.g. Bremmer et al., 2001)

4.3.4 Saccades task

The saccades task mainly yielded two bilateral clusters of activation: a cluster lying at the intersection of the precentral and the superior/middle frontal gyrus corresponding to the localization of the frontal eye field (FEF; Pierrot-Deseilligny, Milea, & Muri, 2004). Activation was also found on the medial surface of the superior frontal gyrus, plausibly corresponding to the supplementary eye field area (Grosbras, Lobel, Van de Moortele, LeBihan, & Berthoz, 1999). The second cluster consisted of parietal areas (superior/inferior parietal lobule, supramarginal/angular gyrus and precuneus). In addition, activation was found in occipital areas (middle occipital gyrus and cuneus/precuneus) and in the cingulate gyrus (see Figure 10).

4.3.5 Overlap

To address the issue of whether common neural structures might be responsible for number as well as for space processing, potentially leading to interactions between these two domains, we tried to identify overlapping neural structures within the clusters described above coding for subtraction, visual motion processing, saccades, and the congruity effect (see Figure 12; Table 7). Strongest indications of overlap were found between the network comprising the neural correlate of the congruity effect and the subtraction task. Bilaterally, activations overlapped in the anterior part of the inferior parietal lobule and in the precuneus. Additional overlap was found in the superior/middle frontal gyrus, in the medial frontal gyrus, and in the precentral gyrus extending into the middle frontal gyrus; but this

was only the case in the right hemisphere (see Figure 12). Except for the spots in the medial frontal gyrus and at the intersection between the precentral and middle frontal gyrus, all of these structures were also activated during the saccades task. This can be seen as a first indication of a recycling of neural circuits that are predominantly specialized for sensori-motor functions (here: saccadic eye movements) for higher cognitive functions, i.e. culturally mediated intellectual functions. Only little indication for overlap with the visual motion processing task was detected around the bilateral spots in the precuneus and in the anterior part of the inferior parietal lobule.

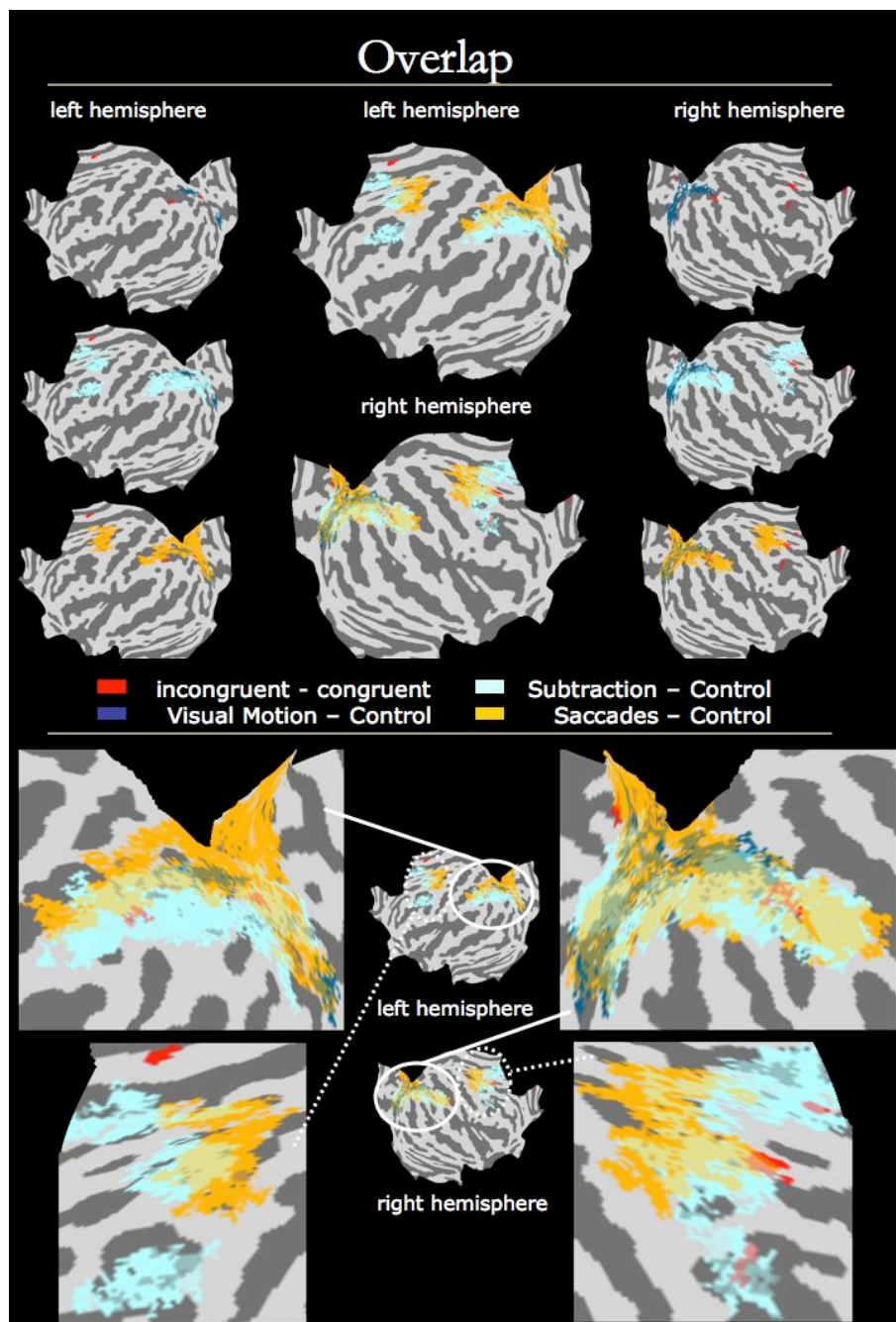


Figure 12. Localization of task-specific and overlapping activations on flattened, cortically aligned hemispheres. The bottom part of the figure contains enlarged depictions of overlap around the intraparietal sulcus (upper row) and in the frontal cortex (lower row).

Table 7

Number of overlapping vertices in the different tasks: numbers in the second column indicate the whole number of vertices activated in the respective task (bold font) or the number of activated vertices in specific parietal structures. Rows in the next columns represent overall overlap (bold font). Detailed information focusing on overlap in different parietal structures is given below.

	Activated vertices	Calculation	Visual motion	Saccades
Congruity effect	218	141 (65%)	2 (1%)	83 (38%)
Inferior parietal lobule	57	56 (98%)	2 (4%)	38 (67%)
Superior parietal lobule	-	-	-	-
Angular gyrus	-	-	-	-
Supramarginal gyrus	4	4 (100%)	-	3 (75%)
Precuneus	42	24 (57%)	-	29 (70%)
Calculation	4265	-	342 (8%)	1966 (46%)
Inferior parietal lobule	1096	-	64 (6%)	542 (49%)
Superior parietal lobule	195	-	75 (38%)	154 (79%)
Angular gyrus	95	-	-	28 (29%)
Supramarginal gyrus	77	-	-	38 (49%)
Precuneus	974	-	186 (19%)	614 (63%)
Visual motion	1070	342 (32%)	-	852 (80%)
Inferior parietal lobule	83	64 (77%)	-	64 (77%)
Superior parietal lobule	276	75 (27%)	-	235 (85%)
Angular gyrus	-	-	-	-
Supramarginal gyrus	-	-	-	-
Precuneus	503	186 (37%)	-	459 (91%)
Saccades	4915	1966 (40%)	852 (17%)	-
Inferior parietal lobule	697	542 (78%)	64 (9%)	-
Superior parietal lobule	589	154 (26%)	235 (40%)	-
Angular gyrus	28	28 (100%)	-	-
Supramarginal gyrus	41	38 (93%)	-	-
Precuneus	1907	614 (32%)	459 (24%)	-

4.4 Discussion

The main goal of the study was to probe the idea that the interaction between number and space processing has its origin in an overlap of neural circuits in parietal cortex, putatively due to a process of “neural recycling” during which cultural achievements (e.g. numerical cognition) co-opt brain areas whose organization fits with the needs of the processes at hand. We conducted an fMRI study with a relatively small voxel size ($2 \times 2 \times 2 \text{ mm}^3$) to identify the neural correlates of a behavioural congruity effect between the processing of numerical and spatial distances that can be seen as an instantiation of the representational link between both domains. In addition, brain areas underlying subtraction, visual motion processing and saccades were examined. This offered the chance to closely look at the mutual neural overlap between different functions.

A reflection of the congruity effect at the neural level was detected in the inferior parietal lobule and the precuneus, such that these areas were more engaged when the external spatial intervals between the numbers of a triplet were not congruent with the numerical intervals, which in turn might reflect their positions on the mental number line. Interestingly, these areas showed substantial overlap with activation maps resulting from the subtraction and the saccades task in parietal cortex. This can be taken as a first indication that indeed the observed interaction between number and space processing has its origin in overlapping neural circuits in parietal cortex. Only little indication of an overlap between the neural correlate of the congruity effect and the visual motion processing task was observed around the bilateral spots in the precuneus and in the inferior parietal lobule. Overlapping activity in the inferior parietal lobule was found for the visual motion processing task and the subtraction task (see Tables 5 and 7), emphasising the assumption of neurons both coding for visual (or even polymodal) motion and quantity (Hubbard et al., 2005). The current results help to further delineate the exact mechanisms guiding numerical cognition and its interplay with spatial representations: neurons in VIP seem predominantly engaged in representing numerical magnitude which is in accordance with the findings of Piazza et al. (2007), who reported that neurons in this area respond to changes in numerosity, irrespective of notation. In addition, our findings

imply that the dynamic interplay between numerical and spatial representations is driven by a neural network comprising anterior intraparietal neurons as well as neurons in posterior regions extending into the precuneus. These structures have been found to be involved in processing numbers and in visuo-spatial tasks like attention orienting, eye movements, grasping, pointing, and mental rotation (Culham & Kanwisher, 2001; Culham & Valyear, 2006; Piazza et al., 2004; Simon et al., 2002; Zago et al., 2001). Since this network was also found to be active during the saccades and the subtraction task in the present study, these circuitries might be the ones assumed to support attentional orientation along a mental number line, as well as along other spatial dimensions (Dehaene et al., 2003; Hubbard et al., 2005). These shifts along a mental number line do not have to be exclusively attentional but may as well involve saccadic eye movements, as has been demonstrated recently (Loetscher et al., 2008). Quantity information, however, seems to be represented by adjacent circuitries that are connected to the aforementioned network (Lewis & Van Essen, 2000). To sum up, the representational crosstalk between number and space processing might have its neural correlate in circuits subserving (covert) attentional shifts and saccadic eye movements but not in neurons coding quantity. Further experiments will have to be conducted to delineate the exact roles of internal or external shifts of attention, as well as overt or planned saccades in the context of numerical cognition tasks.

Additionally, the neural correlate of the congruity effect comprised bilateral activations in the cingulate gyrus and spots in frontal areas including the medial frontal gyrus, the superior/middle frontal gyrus, and in the precentral gyrus of the right hemisphere. Activity in cingulate/frontal areas might be due to monitoring/resolving conflict between stimulus dimensions (Fan, Flombaum, McCandliss, Thomas, & Posner, 2003; Cohen Kadosh, Cohen Kadosh, Henik, & Linden, 2008). Furthermore, right-hemispheric activation in precentral and superior frontal areas might be simply due to more eye movements during incongruent as compared to congruent trials. Given that these regions were also active in the saccades task gives support to this interpretation. On the other hand, this region was also found to be active during the subtraction task where a systematic difference in eye movements is not plausible since all stimuli were presented centrally. We suggest that this activation is due to the recruitment of the sensori-motor system linked to eye movements and saccade planning in the context of mental arithmetic. Indeed, activity in precentral areas might

reflect the use of motor imagery or simulation (Michelon, Vettel, & Zacks, 2006). Moreover, a fronto-parietal circuit incorporating anterior parietal and middle/inferior frontal neurons has been implicated in motor control and imitation (Binkofski et al., 1999; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996) and the precuneus is assumed to be concerned with visuo-spatial imagery (Cavanna & Trimble, 2006), leading us to propose that the neural correlate of the congruity effect might activate a neural network overlapping to some extent with that activated in mental imagery (Zacks, 2008).

In sum, this reasoning points to the idea that numerical cognition relies on a neural network that has evolved phylogenetically to subserve representing and interacting with external space. This way of processing invokes the dynamic updating of spatial relations between objects and the observer, a function presumably relying on a fronto-parietal network that incorporates feedback projections (Colby, 1998). Numerical cognition and calculation might therefore be conceived as operations on a mental number line akin to physical movements along a physical trajectory. Indeed, it could be demonstrated that participants tend to systematically misjudge the outcome of arithmetic problems as a function of the operation (i.e. addition or subtraction). They preferred outcomes that were larger than the actual outcome in addition problems and smaller outcomes than the actual one in subtraction trials (McCrink et al., 2007; Knops et al., 2009). In sum, these findings provide support for the neural recycling hypothesis (Dehaene & Cohen, 2007) according to which culturally mediated functions like arithmetic co-opt phylogenetically older brain circuits and may inherit at least some of their constraints.

5. GENERAL DISCUSSION

Mental number representations were elaborated in this thesis by confronting participants with number triplets spatially and numerically arranged along a line, a so-called “numerical landmark test” (see Figure 4). This paradigm was employed in classical reaction time (RT) experiments examining adults (*Study 1*) and children (*Study 2*) as well as in a neurofunctional investigation using functional magnetic resonance imaging (fMRI; *Study 3*). First of all, the main findings of these different studies will be outlined. Then the focus will be put on theoretical implications of the reported studies and potentials of the numerical landmark test. As far as these issues are concerned, the thesis will end by pointing out possible future research directions.

5.1 Summary of the main findings

In all three studies reported on in this dissertation, the comparison of numerical distances was influenced by the spatial alignment of the numbers, representing a so-called distance congruity effect (DCE). This finding was taken as evidence for a spatial representation of numbers in form of a mental number line (MNL). It was assumed that the DCE is evoked by a facilitation of responses caused by a correspondence between the external format of the spatial alignment of the numbers and the internal mental representation as well as by interfering effects due to a discrepancy of these two spatial arrangements.

Study 1 allowed us to rule out a conflict between assigned responses and response codes elicited by attentional shifts as the mechanism underlying the observed DCE. Moreover, it has been shown that numerical information had no impact when spatial distances had to be compared. These asymmetric findings might be interpreted in terms of relative speed of information processing for the two dimensions or in terms of a parasitic representation of numbers on spatial representations, meaning that established structures representing space are recruited for new uses like number processing.

In *Study 2* children at the age of 8-9 years also exhibited a DCE when being confronted with the numerical landmark test. Correlations between the size of the DCE and calculation abilities were found to be differently marked for girls and boys, leading us to assume that girls and boys in this age make use of different thinking styles in order to solve calculation problems. For boys, who may prefer visuo-spatial thinking styles, a spatial representation of numbers could be helpful when being confronted with addition or subtraction problems, whereas for girls preferring verbal thinking styles it might be even detrimental.

Finally, *Study 3* demonstrated that a neural network mainly comprising parietal and frontal areas is responsible for inducing a DCE in the numerical landmark test. Identifying brain areas coding for subtraction, visual motion processing, and saccades in the same participants, revealed that these activations comprised regions that code for saccades and calculation. They are distinct from but adjacent to areas that presumably code for numerical magnitude. Thus, numerical-spatial interactions may be driven by a network subserving attentional shifts and saccadic eye movements, which is different from the one coding for numerical magnitude. In sum, these findings underline the notion that neural circuitries being involved in updating internal representations of space during eye movements have been “recycled” for accommodating numerical functions and operations (Dehaene & Cohen, 2007).

5.2 Theoretical implications

In the following, the abovementioned results will be discussed in the light of different theoretical positions considering a connection between numerical and spatial representations: the triple-code model of number processing (Dehaene, 1992; Dehaene et al., 1993; Dehaene & Cohen, 1995, 1997) proposes a nonverbal semantic representation of numerical quantity, which might be analogous to a spatial map or number line (Dehaene et al., 2003). The SNARC effect (Spatial-Numerical Association of Response Codes; Dehaene et al., 1993) has been taken as evidence for this view. Dehaene et al. (1993) explained the finding of a SNARC effect in terms of an irrepressible correspondence between the position of response modalities in external space and the position of a respective number on a MNL. Results of the three studies reported in this thesis seem to support this proposal by showing that

spatial distances between visually presented numbers had an influence on the comparison of numerical distances. However, the idea of a direct association between numbers represented on a spatially oriented MNL and a spatial response has been challenged by other accounts.

A model by Gevers et al. (2006) was provided for a detailed conceptualization of the SNARC effect. Most importantly, this model incorporates an intermediate step between the number magnitude and the response representations (see Figure 3). This is in line with the polarity correspondence account by Proctor and Cho (2006) claiming that different polarities are assigned to different stimuli and responses depending on their relative saliency. Here, it is argued that the more salient stimulus and the more salient response are associated with the positive polarity “+” and the less salient with the negative polarity “-”, as long as they can be coded on a bipolar dimension. As a result, both accounts argue in favour of an extra step in which numerical information is categorized before the response side is activated. Numbers are assumed to be first coded as either small (-) or large (+) and this categorical representation of numerical magnitude is then directly (via an automatic route) and indirectly associated (via an intentionally controlled route) with spatially defined responses.

The pivotal question is whether these considerations can be consulted in order to explain the finding of a DCE in the numerical landmark test. In other words, does the finding of the DCE constitute evidence for a MNL or not? Transferring the ideas of the abovementioned “intermediate coding” accounts to the numerical landmark test would mean that categorical representations (small vs. large) of both numerical and spatial distances are established, which in turn induce facilitating effects in case of correspondence and interfering effects when both categorizations do not agree. But in this case it has to be explained, why the spatial dimension is considered when the task instructions do only demand the comparison of numerical distances. A possible explanation might be that the comparison of spatial distances proceeds automatically. This would make sense in terms of a dual-route architecture (e.g. Gevers et al., 2006; Kornblum et al., 1990): numerical and spatial information are processed via two independent pathways, a relatively fast unconditional route coding the spatial information automatically and a relatively slow intentionally controlled route that codes numerical information. If both routes converge on the same response code (congruent condition), a response can be initiated relatively fast. If, on

the contrary, both routes converge on opposing response codes (incongruent condition), reaction times are slower, and errors are more frequent. Results of *Study 1* demonstrated that the comparison of spatial distances was accomplished considerably faster than the comparison of numerical distances, what might be taken as evidence for the assumption of independent pathways coding for numbers and space, respectively. Moreover, the asymmetric effects reported in *Study 1*, demonstrating an influence of the spatial information in the numerical task but no effect of congruity in the comparison task of spatial distances also make sense when assuming that information that is processed automatically (namely the spatial one) can influence the other dimension but not the other way around. In sum, the finding of the DCE can be explained by “intermediate coding” accounts that incorporate a dual-route architecture, but only if one assumes that spatial distances are compared automatically.

Contrasting suggestions have been made according to which spatial as well as numerical information is processed by overlapping pathways and converges on a common representation (Walsh, 2003; Hubbard et al., 2005). In terms of these assumptions, the finding of a DCE in the numerical landmark test might be due to the fact that numerical information cannot be processed independently from the spatial one. Therefore the spatial information does not necessarily have to be processed automatically but instead it might be processed because neural pathways are used for the comparison of numerical distances that are also involved in processing spatial information. In the case of incongruence between the numerical and the spatial dimension, the comparison of numerical distances might be hindered, while it might be facilitated when the information of both dimensions is congruent. Based on this explanation, the asymmetric findings in *Study 1* can be interpreted in terms of a parasitic representation of numbers on spatial representations, implying that established structures representing space might have been recruited for new uses like number processing. That is why it might be possible to process spatial information independently from numerical information, whereas dealing with numerical input might always entail a spatial dimension. However, inferring this from the asymmetric findings of *Study 1* is critical, because it cannot be excluded that these effects are solely due to different task demands. In terms of a relative speed account (Schwarz & Ischebeck, 2003) the degree of cross-dimensional influence depends on the relative time necessary for processing the respective dimensions.

The attribute processed more slowly (e.g. numerical distance) can only induce weaker or even no interference on the dimension, which is processed faster (e.g. spatial distance). Therefore, further experiments providing comparable demands on both dimensions are required in order to resolve this issue.

The idea of a parasitic representation of numbers on spatial representations has also been conveyed for the neural level. In their “neuronal recycling hypothesis”, Dehaene and Cohen (2007) claimed that processing numerical information might rely on neural circuitries in parietal cortex initially developed for coding internal representations of space. More specifically, areas around the hIPS (assumed to play a particular role in the quantity representation of numbers) might coincide with ventral intraparietal (VIP) areas, a region of the human brain that responds to motion in any sensory modality. Flow of activation from this quantity representation in area VIP to interconnected parietal eye field (hLIP) neurons might account for interactions between representations of number and space (Hubbard et al., 2005). This VIP-hLIP circuit seems to play a particular role in updating internal representations of space during eye movements (Duhamel et al., 1992; Medendorp et al., 2003), fuelling the speculation that it is partially “recycled” for mental arithmetic.

In *Study 3* we tried to corroborate these postulates by identifying brain areas coding for subtraction, visual motion processing and saccades in the same subjects. In addition, the neural correlate of the DCE was detected. Overlapping activity in the parietal cortex was mainly found for the subtraction, the saccades and the numerical landmark task. This led us to assume that numerical-spatial interactions can be ascribed to parietal circuitries subserving attentional shifts and saccadic eye movements, which might be the ones proposed to support attentional orientation on a MNL, as well as on other spatial dimensions (Hubbard et al., 2005). Adjacent parietal circuitries were assumed to be responsible for representing visual (or even polymodal) motion and quantity information, but not for inducing numerical-spatial interactions. This, however, does not exclude the notion of overlapping neural circuits in area VIP coding for space, numbers, and even time (see Walsh, 2003). Indeed, single cell recordings in monkeys provided important information regarding this issue. Tudusciuc and Nieder (2007) reported that numerosity and length are encoded by functionally overlapping groups of parietal neurons in the monkey brain. Interestingly, more than half of these quantity-selective neurons were also found to code for visual motion information. In a match-to-sample task monkeys either had to discriminate

lengths of lines or multiple-dot displays with respect to their numerosity. For the overlap neurons, however, the magnitude of the preferred length did not correlate with the magnitude of the preferred numerosity, a finding that might be interpreted as an objection to the idea that magnitude information converges on a common representation in area VIP. In addition, Roitman, Brannon, and Platt (2007) uncovered another type of neural code for numerosity in lateral intraparietal (LIP) areas, where firing rate varied monotonically with numerosity. The authors assumed that these circuits provide ordinal numerical information based on which VIP neurons might compute cardinal numerical representations. This assumption emanates from a strong cross-linking between area VIP and area LIP. Tudusciuc and Nieder (2007) took a step ahead by claiming that the quantity system in the parietal lobe might be part of a broader network of brain areas involved in representing magnitude information. Comparing neural and behavioural responses of the monkeys led them to suggest that the brain does use both firing rate and temporal pattern information when abstract quantity information has to be encoded. According to Tudusciuc and Nieder (2007), information might be decoded in the parietal lobe followed by a readout stage in the prefrontal cortex. This is line with the finding of numerosity-selective neurons in the prefrontal cortex, responding with a longer latency compared to parietal neurons (Nieder & Miller, 2004). In the light of these findings, it appears reasonable to assume that representing and analysing quantity information may not solely be ascribed to parietal neurons but also to neurons in frontal cortex. This fits well with the view of Walsh (2003) arguing that the parietal cortex transforms magnitude information into motor coordinates. Since these sensori-motor transformations make only sense when embedded into a broader neural network incorporating frontal areas for the planning and execution of motor outputs, it is conceivable that neurons in frontal areas reprocess magnitude information provided by parietal circuits. The results of *Study 3* implicated that not only parietal neurons but a neural network mainly comprising parietal and frontal areas seems to be responsible for inducing interactions between number and space processing. Based on these findings, however, it is hard to disentangle specific functions of the different areas being involved. It might be true, that frontal circuits reprocess information provided by parietal neurons. A frontal readout might be necessary in order to maintain information and potentially also to compare specific contents. But at present this is only speculation.

Integrating different lines of research might be helpful to come to a better understanding of the actual mechanisms. Indeed, the neural network coding for the congruity effect corresponds to a large extent with the results of a recent meta-analysis of neuroimaging studies examining mental rotation (Zacks, 2008). It is assumed that mental rotation might depend on a fronto-parietal network with parietal areas fulfilling visuo-spatial image transformations and precentral as well as prefrontal circuits subserving motor simulation (Michelon et al., 2006; Rizzolatti et al., 1996; Zacks, 2008). The relationship between mental rotation and motor simulation is assumed to be understood in terms of how these two processes update different spatial reference frames (see Zacks, 2008): performing mental rotation tasks requires coordinating an object-centred and an environmental reference frame. Object-centred reference frames locate things relative to intrinsic axes of objects. A cupboard, for instance, has a well-defined front, back, bottom, and top. Environmental frames, on the contrary, locate things relative to a larger surrounding area. Relations between these different frames have to be updated constantly while objects are mentally rotated. When comparing two objects this updating is used to align both object-centred reference frames, in order to compare them in a common environmental frame. In some cases an egocentric reference frame, which is defined with respect to the self, comes into play. For instance, when grasping an object, this egocentric frame becomes coupled to the object-based frame of reference. It could be demonstrated that the parietal cortex of monkeys implements a number of finer-grained egocentric reference frames that code for the location of things relative to different body parts. In the monkey brain, area LIP contains representations in eye-centred reference frames, area VIP contains representations in head-centred reference frames, and area AIP (anterior intraparietal) seems to code grasp-related spatial representations. Mechanisms that underlie updating of these different spatial representations presumably reflect the influence of feedback from frontal to parietal cortex (see Colby, 1998). According to Zacks (2008), for some mental rotation tasks an imagined egocentric reference frame might be consulted wherein a rotation of the respective object is simulated, evoking activations of frontal brain areas that plan and execute movements even though there is no motor output.

Comparable mechanisms might be involved in inducing interactions between number and space processing. Seemingly, quantity is represented by parietal neurons in the monkey brain that contain representations in eye-centred (LIP) and in

head-centred (VIP) reference frames. Drawing on *Study 3*, interactions between number and space processing in the human brain are accompanied by activations in anterior parietal neurons as well as neurons in posterior regions extending into the precuneus. Posterior parietal neurons presumably contain representations in eye-centred reference frames, while anterior parietal neurons code grasp-related spatial representations. Interactions between numerical and spatial information might therefore occur in neural networks coding egocentric reference frames that involve eye-centred and grasp-related representations. Activations of grasp-related areas during number processing tasks have already been reported (e.g. Simon et al., 2002; Zago et al., 2001) and were regarded as reminiscent of the use of a finger-counting strategy in childhood (Butterworth, 1999). In addition, it could be demonstrated recently that calculation processes seem to be accompanied by saccadic eye movements (Loetscher et al., 2008). Apparently, we might simulate or even carry out movements in an imagined egocentric space during the comparison of numerical distances, requiring activity of a fronto-parietal network. This idea is not completely new, since it has already been proposed that arithmetic has a quasi-spatial nature analogous to mental manipulations of concrete shapes (e.g. Luria, 1974). What is new is that numerical cognition and calculation might be conceived of as operations on a mental number line akin to physical movements along a physical trajectory. Interestingly, it could be demonstrated that participants tend to systematically misjudge the outcome of arithmetic problems as a function of the operation (i.e. addition or subtraction): they preferred outcomes that were larger than the actual outcome in addition problems and smaller outcomes than the actual one in subtraction trials (McCrink et al., 2007; Knops et al., 2009). But why should we use eye-centred as well as grasp-related representations during number processing? Perhaps finger as well as eye movements provided a basis for imagined movements on a MNL. Movements along such an imagined dimension might have been developed based on our ability to count stepwise by using our fingers. Later on these counting procedures might merely take place in the mind's eye and get replaced or accompanied by eye movements and attention shifts within imagined space. Although adults may have no need for using their fingers or moving their eyes in order to solve calculation problems, neural networks guiding these processes may still be involved during number processing.

As a result, this might imply that the DCE detected in the numerical landmark test reflects different demands on updating processes of an egocentric reference frame, depending on the degree of congruence between external configurations and internal representations of numbers: comparing the two numerical distances might have enforced a transformation of the visually presented information into an imagined egocentric reference frame, namely the MNL. If the externally perceived configuration of the numbers was not in accordance with the mental representation, repeated updating processes of this egocentric reference frame might have been needed. If, on the contrary, both alignments were congruent, less updating processes might have been necessary. See Figure 13 for a detailed description of possible mechanisms underlying the DCE.

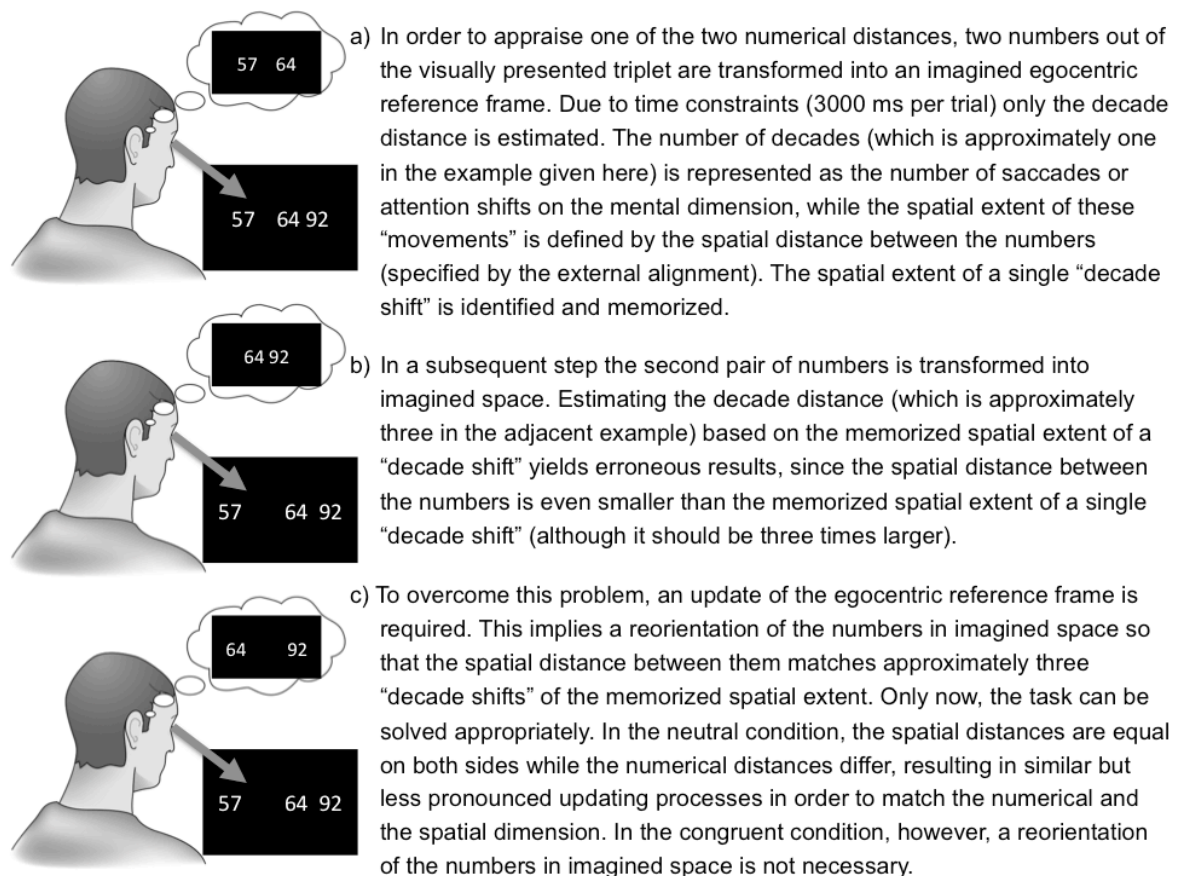


Figure 13. Proposal on the mechanisms underlying the DCE.

In an analogous manner to mental rotation processes, the aforementioned mechanisms might involve a fronto-parietal network with parietal areas fulfilling visuo-spatial image transformations within an egocentric reference frame and frontal circuits subserving movements along this imagined dimension. A strong cross-linking between these areas might be important for updating processes. However, further studies are needed to substantiate these considerations. Tracking eye movements during the comparison of numerical distances might help to gain more insight into the processes at hand. Applying this method might, for instance, offer the chance to test whether the number triplets are decomposed in two pairs processed in succession. Moreover, a sequential presentation of the three numbers constituting a triplet might be an interesting modification of the numerical landmark test. Finding a DCE in this modified version would provide evidence for the assumption that the spatial variations are memorized in combination with the numerical information.

In sum, the abovementioned considerations give reason to assume that during the numerical landmark test an imagined egocentric reference frame might be consulted wherein movements in order to compare numerical distances are executed, evoking activations of a fronto-parietal network. This argues for the existence of a spatial representation of numbers in form of a MNL. These considerations need to be substantiated and it has to be examined whether the assumed mechanisms apply specifically to the numerical landmark test or if they can be transferred in order to explain other findings implying a link between number and space processing e.g. the SNARC effect (Dehaene et al., 1993), attention shifts induced by numbers (Fischer et al., 2003), or disruptions of mental number representations in neglect patients (Zorzi et al., 2002). So far, the question of the underlying principles of interactions between number and space processing cannot be specified unequivocally. Importantly the focus of future studies should not only be set on specific neural structures but also on the interplay between them.

Based on the fact that the DCE represents evidence for the existence of a MNL, results of *Study 2* can be viewed as a demonstration of spatial number representations in children at the age of 8-9 years. As can be seen in Figure 14, however, not all of the 100 children exhibited a DCE in the numerical landmark test. A group of 42 children showed a DCE based on reaction times (RT) as well as on error rate (ER), another 48 children exhibited a DCE on one of these dimensions, and in a group of 10 children no DCE was detected at all. In contrast, most of the adults

(91 %, see Figure 15) participating in *Study 1 or 3* exhibited a DCE on both dimensions.

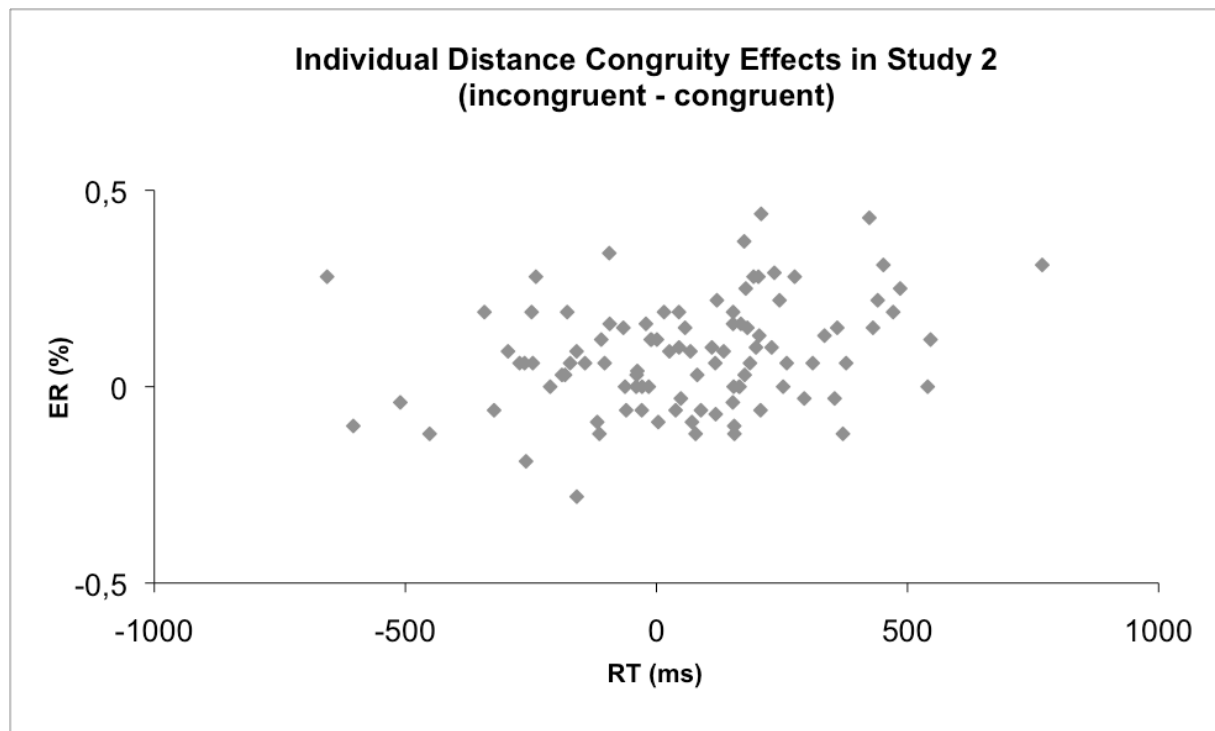


Figure 14. Mean difference values (incongruent condition – congruent condition) computed for each participant in Study 2 ($n = 100$) for reaction times (RT) and for error rate (ER) with positive values indexing the DCE.

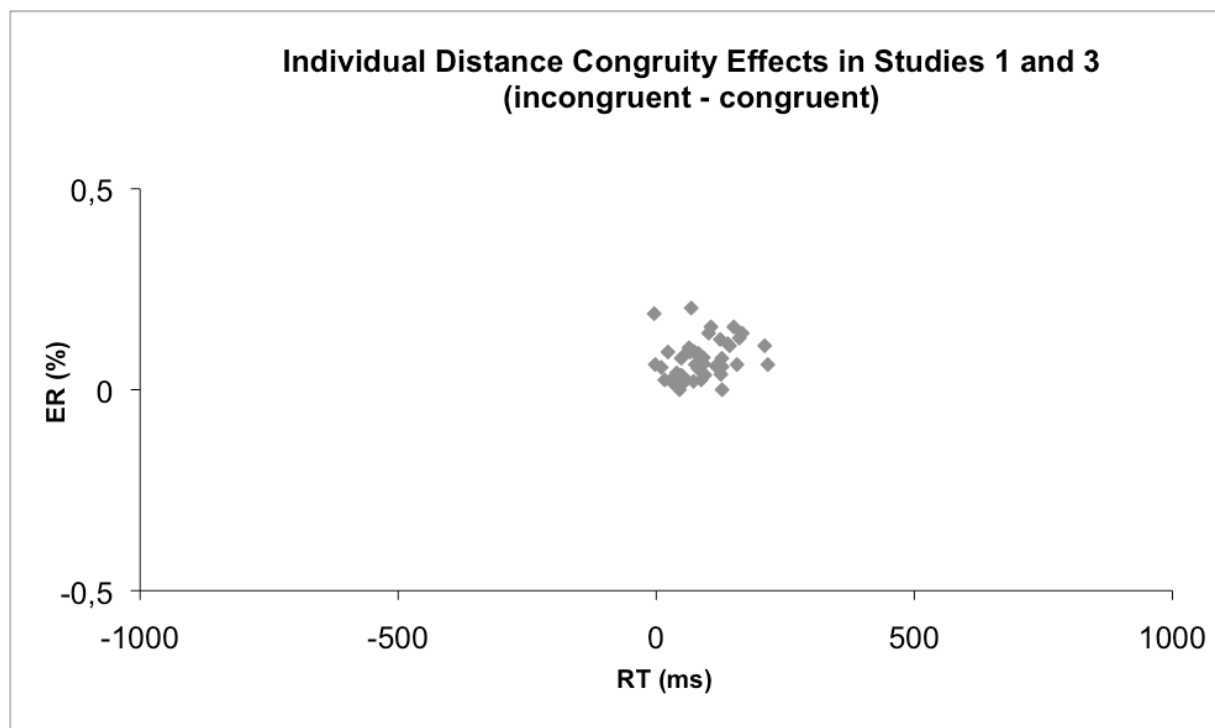


Figure 15. Mean difference values (incongruent condition – congruent condition) computed for each participant in Studies 1 and 3 ($n = 45$) for reaction times (RT) and for error rate (ER) with positive values indexing the DCE.

These findings might suggest that aspects of spatial number representations are influenced by experience, culture or instruction. Indeed, number lines are instantiated on rulers, thermometers, tape measures, and other measuring devices. Children may therefore learn the mapping of number to space over the course of mathematics instruction and everyday experience. A recent study by de Hevia & Spelke (2009) demonstrated, however, that non-symbolic spatial and numerical information interacts in children prior to the onset of formal instruction and shows little change in the strength of the interaction after 5 years of age. Accordingly, it cannot be excluded that humans possess an unlearned, automatic, and non-directional mapping of number to space, whose direction may be fixed by experience.

Interestingly, we found a connection between spatial representations of numbers in children and mathematical abilities, emphasising a special role of the spatial nature of semantic number representations. Results of *Study 2* demonstrated that boys at the age of 8-9 years, who represented numbers spatially, seemed to be those with better calculation skills. But this was not true for girls in this age. When being confronted with addition or subtraction problems those girls who did not represent numbers spatially tended to outperform girls who did. This finding adds a new dimension, which is mostly neglected in models of number processing, namely individual differences in the way of dealing with numbers. We assume that girls and boys make use of different thinking styles in order to solve calculation problems. For boys, who may prefer visuo-spatial thinking styles, a spatial representation of numbers might be helpful when being confronted with addition or subtraction problems, whereas for girls preferring verbal thinking styles it might be even obstructive. Similar proposals have already been raised. For instance, the “preferred entry code hypothesis” introduced by Noël and Seron (1992, 1993) according to which numbers are always transferred to a preferred representation. The nature of this representation is assumed to differ individually. A “verbal type” represents numbers in a word-form, whereas a “visual type” uses an Arabic representation. Evidence for this assumption comes from fMRI studies demonstrating individual

differences in activation patterns during mental calculation (Burbaud et al., 2000; Rueckert et al., 1996). Moreover, it has been demonstrated that arithmetic processing seems to be shaped by cultural influences. While native English speakers largely employ language processes for mental calculation, native Chinese speakers, engage visual processes for the same task (Tang et al., 2006). The authors suggest that these findings might be due to different experiences during reading acquisition and other cultural factors such as mathematics learning strategies. Learning to read Chinese characters, for example, puts high demands on visuo-spatial processes because various configurations have to be learnt and memorized. The use of the abacus in many Asian schools may also contribute to a visuo-spatial conceptualization of numbers. In sum, there is considerable evidence for the fact that differences in the way of dealing with numbers seem to exist. But up to now, it is not clear, where these differences stem from. They might be due to cultural factors like reading experience or mathematics learning strategies, while also biological conditions like gender might play a role. Furthermore, it is still unclear whether only the way of dealing with numbers or even the nature of the underlying representation differs individually. All in all, the aforementioned considerations depart from the still existing separation of experimental psychology and the study of individual differences (see Cronbach 1957, 1975 for a discussion on this separation), and this departure might be necessary in order to develop a deeper understanding of numerical cognition.

Overall, there are some theoretical implications that can be derived from this dissertation. First of all, results of *Study 1* underline the assumption that number representations might be built on spatial ones, leading us to think about numbers in spatial terms. As has been pointed out by *Study 2*, however, individual differences in the way of dealing with this kind of spatial number representations seem to exist. Finally, based on the findings of *Study 3* it can be assumed that numerical-spatial interactions arise from a neural network subserving attentional shifts and saccadic eye movements, which might also be involved in calculation. Therefore, theoretical conceptions of numerical cognition should incorporate a spatial nature of our number representations and of our mental calculation strategies, as well as the existence of individual differences.

5.3 Potentials of the numerical landmark test

Originally the landmark test, requiring the comparison of two segments of pre-bisected lines (see Milner et al., 1993) is used to assess perceptual neglect. The modified version applied in the different studies of this thesis provided robust behavioural evidence for an interaction between numerical and spatial information in form of a DCE (see Figure 15). Providing the congruity effect as a robust indicator of interactions between the processing of numerical and spatial distances, the numerical landmark test may be useful to yield a more precise picture of mental number representations. In all of the studies conducted for this thesis the different numbers constituting a triplet in the numerical landmark test were always aligned in ascending order, because several studies suggest that mental representations of numbers entail a spatial organization in form of a line going from left to right (at least in left-to-right reading cultures). However, other alignments of mental number representations might exist as well. Different variations of the numerical landmark test might help to shed more light on this topic. For instance, the three numbers constituting a triplet can be arranged in descending order to examine a possible right-to-left organisation of mental number representations. Moreover, presenting the different triplets vertically instead of horizontally might reveal top-to-bottom or bottom-to-top representations.

Beside these numerical and spatial modifications, the numerical landmark test might also be useful to further examine the claim by Walsh (2003) that numbers, space and time are part of a generalized magnitude system. Instead of presenting the three numbers constituting a triplet simultaneously, they can also be shown in succession. Congruent, neutral and incongruent stimuli can be created by varying temporal and numerical distances independently. As a result, possible interactions between the numerical and the temporal dimension can be investigated. Perhaps it might be even possible to reveal interactions between all the three dimensions in a more complex design. For example, the respective numbers can be presented consecutively (with different temporal intervals) on different positions on screen without disappearing.

As mentioned above, a landmark test, in which two segments of pre-bisected lines have to be compared with regard to their length, is used to diagnose perceptual neglect. The modified version employing numbers may also be helpful in this area. It is conceivable to gain more insight into a possible association between perceptual and representational forms of the neglect phenomenon by looking for interactions between the spatial (perceptual) and the numerical (representational) dimension in these patients.

Finally, another modification of the numerical landmark test may also be suitable to clarify the question whether the link between numerical and spatial representations is based on cultural conventions, or whether it might be due to an undifferentiated magnitude system predispositioned for spatial and numerical transformations and possibly present since birth (Izard et al., 2008). Indeed, all humans, regardless of their culture and education seem to possess an intuitive understanding of number. There is considerable behavioural evidence suggesting that numerical competence may be present early on in infancy (see Feigenson, Dehaene, & Spelke, 2004 for an overview). Young children can compare sets represented by dot arrays on the basis of number. At six months for instance, children seem to be able to distinguish items at a ratio of 1:2 (Xu & Spelke, 2000). In these studies of number discrimination, infants are typically habituated to a display representing one numerosity, and then a new numerosity is shown. In case of dishabituation, it is assumed that children can distinguish the two quantities.

A modified version of the numerical landmark test might offer the chance to look for interactions between numerical and spatial representations in children early after birth. Since children at this age are not able to process symbols like Arabic digits, numerical information has to be presented in a non-symbolic form like arrays of dots representing different quantities. By also varying the length of these arrays, congruent (e.g. **ooo** vs. **oooo**) and incongruent pairs (e.g. **o o o** vs. **oooo**) can be created. A similar experimental setup has already been used in adults demonstrating that the spatial cues interfered with the processing of numerosity (Dormal & Pesenti, 2007). Habituating infants to either congruent or incongruent pairs and looking for dishabituation due to the presentation of a deviant arrangement (incongruent or congruent) of the triplet might be an interesting possibility to shed more light on representational structures in this age.

5.4 Future directions

This final section will delineate possible future research directions. Suggestions how to further investigate the underlying principles of interactions between number and space processing and potentials of the numerical landmark test have already been outlined in the preceding sections. Picking up the last point, namely, the proposal to examine children early after birth with a modulated version of the numerical landmark test is a nice starting point for developing further ideas that might be interesting to work on in the future.

After looking at possible interactions between numerical and spatial representations in children early after birth, longitudinal studies focusing on developmental aspects of spatial number representations and their connection with higher-order arithmetical and mathematical concepts might be worthwhile. If possible, these studies might not only be carried out on a behavioural but also on a neural level. As has been pointed out earlier in this dissertation, individual differences in the way of dealing with numbers might well exist. Therefore, developmental as well as studies in adults should also take this into consideration.

Furthermore, the idea of conceiving numerical cognition and calculation as mental operations akin to physical movements is another interesting hint deriving from this dissertation, which coincides well with current lines of research. Indeed, ideas going back to Piaget (1952) who claimed that thought develops from action are revived in a new research domain called embodied cognition. Focusing on this interesting topic might enhance our understanding of number processing, calculation, or generally of thought.

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APPENDIX

Appendix A: Item-specific performance (mean reaction times for correct responses in ms and percentage of errors) in the numerical landmark test in Study 2 as a function of the factor congruity (congruent vs. neutral vs. incongruent) with standard deviations in parentheses.

Triplet		Congruent	Neutral	Incongruent
24 45 59	RT in ms	2617 (615)	2458 (680)	2491 (759)
	Errors in %	32 (34)	32 (35)	43 (34)
27 55 62	RT in ms	2444 (698)	2469 (662)	2454 (630)
	Errors in %	30 (32)	35 (35)	35 (35)
28 42 63	RT in ms	2571 (742)	2425 (768)	2439 (785)
	Errors in %	45 (35)	49 (35)	52 (37)
31 38 66	RT in ms	2323 (607)	2077 (573)	2371 (532)
	Errors in %	18 (26)	11 (22)	23 (31)
34 62 69	RT in ms	2305 (570)	2444 (686)	2452 (688)
	Errors in %	24 (32)	31 (33)	32 (34)
37 51 72	RT in ms	2583 (758)	2358 (722)	2280 (672)
	Errors in %	57 (37)	58 (39)	53 (35)
38 59 73	RT in ms	2635 (785)	2447 (790)	2543 (788)
	Errors in %	64 (34)	65 (34)	66 (36)
43 71 78	RT in ms	2224 (526)	2268 (547)	2332 (605)
	Errors in %	15 (24)	18 (28)	20 (30)
47 68 82	RT in ms	2467 (665)	2498 (837)	2431 (781)
	Errors in %	54 (38)	62 (36)	67 (37)
48 55 83	RT in ms	2437 (682)	2601 (660)	2426 (729)
	Errors in %	24 (31)	26 (34)	38 (35)

51 65 86	RT in ms	2342 (619)	2348 (639)	2753 (753)
	Errors in %	20 (30)	24 (29)	39 (36)
52 59 87	RT in ms	2237 (547)	2323 (656)	2318 (566)
	Errors in %	14 (27)	17 (26)	15 (24)
56 84 91	RT in ms	2257 (723)	2553 (594)	2554 (593)
	Errors in %	20 (28)	37 (36)	35 (30)
57 64 92	RT in ms	2327 (598)	2329 (692)	2583 (600)
	Errors in %	19 (29)	25 (30)	22 (30)
61 82 96	RT in ms	2357 (548)	2411 (507)	2570 (683)
	Errors in %	27 (34)	38 (37)	40 (35)
62 76 59	RT in ms	2385 (590)	2400 (584)	2369 (671)
	Errors in %	20 (27)	21 (31)	34 (35)

Appendix B: Pearson correlations between raw average RT (only correct responses) and error data for congruent as well as incongruent conditions in the numerical landmark test in Study 2 and calculation abilities, performance in the VMI-copying task, performance in the VMI-visual-discrimination task, for all participants and separately for girls and boys.

		RT congruent	RT incongruent	Error rate congruent	Error rate incongruent
Calculation abilities	overall:	-0.23*	-0.12	-0.34**	-0.20*
	girls:	-0.11	-0.10	-0.17	-0.38**
	boys:	-0.30	-0.07	-0.53**	-0.16
VMI- copy task	overall:	-0.02	0.12	-0.34**	-0.13
	girls:	-0.02	0.11	-0.47**	-0.03
	boys:	-0.04	0.12	-0.23	-0.25
VMI- discrimination task	overall:	0.16	0.17	-0.22*	-0.21*
	girls:	0.14	0.14	-0.37**	-0.11
	boys:	0.15	0.16	-0.06	-0.32*
RT congruent	overall:		0.74**	0.03	-0.13
	girls:	-	0.75**	-0.07	-0.14
	boys:		0.75**	0.14	-0.08
RT incongruent	overall:			-0.19	0.09
	girls:	-	-	-0.27*	-0.13
	boys:			-0.09	0.06
Error rate congruent	overall:				0.23*
	girls:	-	-	-	0.33*
	boys:				0.13

* $p < 0.05$, ** $p < 0.01$ (two-sided); $n = 100$ (58 girls, 42 boys)

Appendix C: The red rectangle represents the area that was covered during the functional measurement in Study 3 in a mid-sagittal slice of one of the participants.



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EIDESSTATTLICHE ERKLÄRUNG

Hiermit erkläre ich an Eides statt, dass die vorgelegte Dissertation

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von mir selbst und ohne andere als die angegebenen Hilfsmittel angefertigt wurde.

Diese Dissertation wurde in der jetzigen oder in einer ähnlichen Form noch bei keiner anderen Hochschule eingereicht und hat noch keinen sonstigen Prüfungszwecken gedient.

Frankfurt am Main, den 18.03.2010

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