Evaluating domain-specific numerical and domain-general contributions to number processing

Combining temporal dynamics and neurofunctional correlates

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Summary

The Triple Code Model (TCM) is the most prominent and influential model of numerical cognition and its neurocognitive foundations. Relying on experimental psychological, neuropsychological, and neurofunctional data, its major contribution for a better understanding of number processing is the assignment of domain-specific structure-function-relationships to the proposed numerical codes. The TCM assumes three distinct codes which interact bi-directionally with each other but can be selectively impaired: a visual Arabic number code attributed to bilateral fusiform gyrus, an auditory verbal code associated with left perisylvian language areas, and an analogue magnitude code to be found in bilateral intraparietal sulcus (IPS). Thus, domain-specific functions are associated with specific neural structures. Nevertheless, two important aspects were less in the focus of the TCM: On the one hand, the involvement of domain-general processes and their complex interplay with domain-specific processes involved in numerical cognition received only little attention. On the other hand, as a structural model the TCM describes the processes involved in numerical cognition with high spatial resolution based on neuropsychological and neurofunctional data, while temporal aspects were left largely unnoticed so far. However, research of recent years emphasized the relevance of both the complex interplay of domain-specific and domain-general processes as well as good spatial and good temporal resolution of these processes to adequately understand processes and mechanisms involved in numerical cognition.

To pursue this issue, the present thesis focused on these so far underspecified issues in two sections. As part of the tertiary association cortex, bilateral IPS is not only involved in domain-specific number processing, but also in other rather domain-general cognitive functions. For this reason, Section 1 addresses domain-specific numerical and domain-general processes in parietal cortex involved in numerical cognition in two fMRI and one behavioral study with the aim to complement functions associated with the parietal cortex by the TCM. Section 1 shows that i) relative magnitude information is processed comparably to absolute magnitude information in intraparietal brain areas, ii) parietal brain regions are also involved in domain-general processes related to, but beyond magnitude processing, and iii) specific aspects of complex number concepts (e.g., multi-symbol numbers) are associated with space only with increasing experience with this specific concept. Section 2, for its part, focuses on aspects of temporal dynamics of number processing distinguishing between early automatic bottom-up mechanisms on the conceptual level and later cognitively controlled top-down mediated processes as revealed by eye-tracking.

Based on the present findings and the existing literature, a model extension of the TCM is proposed, which aims at specifying the assumptions of the TCM for domain-specific numerical and domain-general processes (principally independent from temporal aspects and time-critical methods) and enriching the TCM with early bottom-up and later top-down mediated processing stages (based on findings of time-critical methods). In doing so, three distinct processing stages are assumed: an initial visual input stage in occipital brain areas, an early largely automatic and stimulus-driven conceptual processing stage in parietal regions, and a later top-down and cognitively controlled processing stage recruiting fronto-parietal areas.

This model extension provides a first attempt to complement neurofunctional correlates of domain-specific numerical and domain-general processes with aspects of temporal dynamics of number processing.

Zusammenfassung

Das Triple Code Model (TCM) ist das bekannteste und einflussreichste Modell, das zur Charakterisierung numerischer Kognition und deren neurokognitiver Grundlagen herangezogen wird. Anhand experimentalpsychologischer, neuropsychologischer und neurofunktioneller Daten ordnet das TCM neuronalen Strukturen domänenspezifische Funktionen zu. Hierbei unterscheidet das TCM zwischen drei numerischen Repräsentationsformen, die miteinander interagieren, aber unabhängig voneinander gestört sein können: einer visuellen Repräsentation arabischer Zahlen, die bilateral im Gyrus fusiformis verortet wird, einer auditorisch-verbalen Repräsentation assoziiert mit linkshemisphärischen perisylvischen Sprachareal en sowie einer abstrakten Größenrepräsentation, die im bilateralen intraparietalen Sulcus (IPS) beheimatet sein soll. Zwei wichtige Aspekte standen bisher allerdings nicht im Fokus des TCM: Zum einen erhielten domänenübergreifende Prozesse und deren komplexes Zusammenspiel mit domänenspezifischen Prozessen nur wenig Aufmerksamkeit. Zum anderen beschreibt das TCM die beteiligten Prozesse zwar mit einer hohen räumlichen Auflösung, berücksichtigt aufgrund der verwendeten Untersuchungsmethoden allerdings nicht die zeitliche Komponente. Die Forschung der letzten Jahre hat jedoch die Relevanz beider Aspekte hervorgehoben: Um die in der numerischen Kognition involvierten Prozesse und Mechanismen umfassend verstehen zu können, ist es notwendig, sowohl die Interaktion zwischen domänenspezifischen und domänenübergreifenden Prozessen als auch die räumliche *sowie* die zeitliche Auflösung dieser Prozesse zu untersuchen. Aus diesem Grund konzentriert sich die vorliegende Arbeit in zwei Abschnitten auf diese bisher unterspezifizierten Aspekte.

Als Teil des tertiären Assoziationskortexes ist der bilaterale IPS nicht nur an der domänenspezifischen Verarbeitung numerischer Größe beteiligt, sondern auch an domänenübergreifenden kognitiven Funktionen. Deshalb beschäftigt sich der erste Abschnitt dieser Arbeit in zwei fMRT- und einer Verhaltensstudie mit domänenspezifischen numerischen und domänenübergreifenden parietalen Prozessen, die in die numerische Kognition involviert sind, mit dem Ziel, die vom TCM vorgeschlagenen Funktionen für den parietalen Kortex zu erweitern. Dieser erste Abschnitt zeigt, dass i) relative Größeninformation vergleichbar mit absoluter Größeninformation in intraparietalen Hirnarealen verarbeitet wird, ii) parietale Regionen auch an domänenübergreifenden Prozessen beteiligt sind, die über reine Größenverarbeitung hinausgehen und iii) bestimmte Aspekte komplexer numerischer Konzepte (z.B., positive und negative Zahlen) erst mit zunehmender Erfahrung mit einer spezifischen Seite im Raum assoziiert werden. Der zweite Abschnitt konzentriert sich hingegen auf Aspekte der zeitlichen Verarbeitung, über welche das TCM als Strukturmodell bislang keine explizite Auskunft gibt. Auf der Grundlage von Eye-tracking Daten wird zwischen frühen automatisierten bottom-up Prozessen und späteren kognitiv kontrollierten Verarbeitungsschritten unterschieden.

Anhand der vorliegenden Ergebnisse und der vorhandenen Literatur wird eine Modellerweiterung des TCM vorgeschlagen, in der die Annahmen des TCM für domänenspezifische numerische und domänenübergreifende Prozesse (prinzipiell unabhängig von zeitlichen Aspekten und zeitkritischen Methoden) spezifiziert und durch frühe automatisierte und spätere kognitiv kontrollierte Verarbeitungsschritte (basierend auf zeitkritischen Methoden) verfeinert werden sollen. Hierbei wird zwischen drei Verarbeitungsstufen unterschieden: Eine Stufe für den visuellen Input in okzipitalen Hirnregionen, eine frühe, weitgehend automatisierte Verarbeitungsstufe in parietalen Arealen sowie eine spätere top-down und kognitiv kontrollierte Stufe in fronto-parietalen Regionen.

Diese Modellerweiterung stellt einen ersten Versuch dar, sowohl die neurofunktionalen Korrelate domänenspezifischer numerischer und domänenübergreifender Prozesse als auch zeitliche Aspekte für die Beschreibung der Zahlenverarbeitung zu berücksichtigen.

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PART I: INTRODUCTION

General introduction

The Triple Code Model (TCM) is the most influential theoretical framework of numerical cognition integrating cognitive and neuro-cognitive data into an anatomo-functional model of number processing (Dehaene, 1992; Dehaene & Cohen, 1995, 1997; Dehaene et al., 2003). The major contribution of the TCM is unquestionably the description of domain-specific structure-function-relationships for the domain of numerical cognition. It assumes three distinct codes in which numerical information is processed in the brain: a visual Arabic number code in bilateral fusiform gyri, in which quantities are recognized visually, an auditory verbal code in left perisylvian language areas and left angular gyrus (AG), in which language-mediated facts are stored and numbers are processed verbally, and an analogue magnitude code in bilateral intraparietal sulcus (IPS), in which semantic magnitude information is represented like on a spatially oriented number line (Dehaene et al., 2003). Yet, as part of the tertiary association cortex the parietal cortex in particular is not only involved in domain-specific numerical processes but also in rather domain-general processes (Critchley, 1953; Culham & Kanwisher, 2001; Humphreys & Lambon Ralph, 2015, 2017). However, domain-general influences have only been dealt with marginally as the TCM proposed them to be represented in frontal areas.

Furthermore, based on neuropsychological and neurofunctional data, the focus of a structural model like the TCM was less on the description of temporal aspects of number processing. However, recent research using time-critical neuro-cognitive methods emphasized the relevance of good temporal resolution to describe the underlying cognitive processes in numerical cognition (Dehaene, 1996; Kiefer & Dehaene, 1997; Avancini, Soltesz, & Szucs, 2015; Teichmann, Grootswagers, Carlson, & Rich, 2018; Pinheiro-Chagas, Piazza, & Dehaene, 2019. Importantly, eye-tracking provides an additional complementary approach to differentiate between early and late processing stages (Calvo & Meseguer, 2002; Deutsch, Frost, Pelleg, Pollatsek, & Rayner, 2003; Joseph et al., 2008; Just & Carpenter, 1980).

The present thesis addresses these two aspects in two sections. In Section 1, I aim at specifying domain-specific numerical and domain-general parietal processes involved in number processing. It includes three studies which focus on distinct assumptions of the TCM for the parietal cortex. In two fMRI and one behavioral study, I will examine the propositions of the TCM by i) extending it for domain-specific numerical processes for relative magnitude information, ii) investigating the influence of domain-general processes during number processing located in the parietal cortex on the neural level, and iii) testing the automatic association of numbers and space. In Section 2, I aim at evaluating aspects of the temporal dynamics of the processes involved in numerical cognition. Eye-tracking studies on number processing are reviewed and discussed with the aim of distinguishing early automatic mechanisms from later, rather cognitively controlled processes involved in number processing. I will then use the results of these two sections to propose an extension of the TCM including domain-specific numerical and domain-general processes as well as aspects of their temporal dynamics. The integration of the present findings is a first attempt to complement specific neurofunctional correlates of domain-specific numerical and domain-general processes with aspects of temporal dynamics of number processing.

1 Numbers rule the world

Numbers are omnipresent in all areas of modern life. We start in the morning with a look at the clock and end with setting the alarm clock in the evening. In between, we make phone calls, use quantity information from recipes for baking or cooking, take a certain bus line at a specific time, check our account balance, and keep our fingers crossed for our favorite club to score high enough to climb up the league tables.

For all these activities, we have to be able to understand and to reason with numbers. However, when we are not capable to handle numbers appropriately, this will cause problems not only in our private life. Not to mention problems at school, poor numeracy skills have an impact on the economic, social, and health status of affected individuals (e.g., Litster, 2013). In particular, difficulties with numbers are linked to reduced employment opportunities, lower salaries, increased risks of involvement with the criminal justice system, as well as increased health risks (Gross, Hudson, & Price, 2009; Litster, 2013; Parsons & Bynner, 2005). This, in turn, does not only impact the respective individuals, but also causes enormous societal costs (Gross et al., 2009; OECD, 2010). The costs related to individuals with numeracy or math difficulties are estimated at up to £763 million each year in the United Kingdom for educational, low wages, and health costs as well as costs of crime (Gross et al., 2009). Importantly, numeracy is a stronger determinant than literacy as regards improvements to employment status (Litster, 2013). Also for this reason, interest in research on the cognitive underpinnings of number processing increased steadily in recent years.

The description of how numerical information is cognitively represented and processed is a key point in numerical cognition research. By means of different methods such as reaction time experiments, eye-tracking measures, electroencephalography (EEG), event-related potentials (ERPs), or functional brain imaging (fMRI, PET, MEG) in typically functioning and cognitively impaired individuals, it is possible to investigate different aspects of number processing. Various models have been proposed that describe cognitive performance of normal and impaired number processing based on this research. The Triple Code Model (TCM) of numerical cognition by

Dehaene (1992) and its successors (e.g., Dehaene & Cohen, 1995, 1997; Dehaene et al., 2003; Dehaene, 2009) is currently the most prominent model about number processing and calculation. It assumes three distinct codes in which numerical information is processed within the brain: an analogue magnitude code in which semantic quantity information is represented like on a spatially oriented mental number line, an auditory verbal code in which numbers are processed verbally and language-mediated facts are stored, and a visual Arabic number code in which numbers and quantities are visually recognized. Based on lesion and functional imaging data, these codes were assigned to neural correlates in bilateral parietal cortex (analogue magnitude code), left-hemispheric perisylvian language areas and left angular gyrus (auditory verbal code), and bilateral fusiform gyri (visual Arabic number code; Dehaene & Cohen, 1995, 1997; Dehaene, Piazza, Pinel, & Cohen, 2003).

As a classical box-and-arrows model of cognitive neuropsychology with the primary interest on structural propositions and domain-specific aspects of numerical processing, the TCM mainly focuses on the description of domain-specific structure-function-relationships. Domain-general processes have only been dealt with marginally as the TCM does not specify these processes but proposes domain-general influences to be represented in frontal brain regions. Yet, it is only possible to understand human, and thus also numerical, cognition when complex interactions between domain-specific and domain-general processes in flexibly interconnected networks are investigated and understood (Reinvang, 1985; Catani & Ffytche, 2005; Catani, 2011). Importantly, as part of the higher order (tertiary) association cortex, bilateral IPS is not specifically dedicated to number processing, but rather involved in domain-general processes (Critchley, 1953; Culham & Kanwisher, 2001; Humphreys & Lambon Ralph, 2015, 2017). Nevertheless, it was shown in electrophysiological studies that single neurons in intraparietal areas in macaques responded differently to distinct numbers of items (Nieder, Diester, & Tudusciuc, 2006; Roitman, Brannon, & Platt, 2007). Based on co-localizations and overall similarities with the topological arrangement of the intraparietal regions in macaques and humans, a homology between the brain regions activated by numerical tasks in humans and macaques was suggested (Castaldi, Vignaud, & Eger, 2019; Nieder et al., 2006). This indicates that IPS itself seems to comprise both domain-general and domain-specific (sub-)regions. Thus, the complex interplay between domain-general and domain-specific processes needs to be investigated to understand the underlying processes involved in numerical cognition.

Furthermore, based on neuropsychological and neurofunctional data, the TCM provides relatively good spatial resolution of structure-function-relationships in the human brain. In fact, this is a major contribution of the TCM, while temporal aspects of the involved processes were less in the focus of structural models like the TCM. Yet, in an early study Dehaene (1996) showed that temporal processing stages indeed were of interest. Dehaene (1996) combined ERPs with an additive-factors method (Sternberg, 1969) to differentiate between the processing stages in a number comparison task. Recently, studies on the temporal dynamics of number processing and mental arithmetic have increased using EEG/ERPs (Avancini et al., 2015; Kiefer & Dehaene, 1997; Hsu & Szucs, 2012; Jost et al., 2004; Hinault & Lemaire, 2016), magnetoencephalography (MEG; Teichmann et al., 2018; Pinheiro-Chagas et al., 2018), and electrocorticography (ECoG; Shum et al., 2013; Daitch et al., 2016). Thus, the growing interest in the temporal dynamics in numerical cognition supports the assumption that it is not only necessary to pinpoint the neural underpinnings with good spatial resolution to understand the complex interplay of domain-specific and domain-general processes more fully. Rather, both good spatial as well as good temporal resolution are needed to comprehensively and adequately grasp the processes in numerical cognition. Unfortunately, so far available methods do not allow to simultaneously accomplish both good temporal *and* spatial resolution by means of only one method. However, it is possible to combine methods with good spatial or good temporal resolution to better understand the underlying mechanisms in numerical cognition.

Importantly, there are possibilities to capture and account for the temporal sequences of cognitive processes (e.g., Sternberg, 1969; Dehaene, 1996). Reading research has highlighted the benefit of using eye-tracking, which provides a complementary approach to distinguish between early and later processing steps during reading (Calvo & Meseguer, 2002; Deutsch, Frost, Pelleg, Pollatsek, & Rayner, 2003; Joseph et al., 2008; Just & Carpenter, 1980). Although several eye-tracking studies were carried out in the domain of numerical cognition, the findings of neurofunctional, reaction time, and eye-tracking experiments have not yet been amalgamated into one theoretical framework describing the temporal dynamics of number processing in an integrated way.

Therefore, it was the aim of the present thesis to specify aspects of the temporal dynamics and the neural correlates of domain-general and domain-specific numerical processing in order to propose an integrated model extension of the TCM.

To pursue this aim, four studies were conducted, relying on different methods and distinct populations. The studies are grouped in two sections: Section 1 aims at investigating domain-specific numerical and domain-general parietal processes involved in number processing. It includes three studies that specifically address specific propositions of the TCM for the parietal cortex. Study 1 aimed at extending the scope of an analogue magnitude code to relative magnitude, Study 2 examined the involvement of parietal cortex in processing magnitude understanding and beyond, whereas Study 3 aims at investigating the automatic association of numbers and space. Section 2, for its part, focuses on temporal dynamics of number processing. Exploiting the success of reading research, eye-tracking studies on number processing are reviewed and discussed to allow separating the underlying cognitive processes into early and late processing steps in Study 4.

In the following, the TCM will be introduced in more detail as a theoretical basis for the research questions of the present thesis before the theoretical background for the research questions of Sections 1 and 2 will be presented.

2 The Triple Code Model

The Triple Code Model (Deheane, 1992), its extension to an anatomo-functional model (Dehaene & Cohen, 1995) and its further specifications (Dehaene & Cohen, 1997; Dehaene et al., 2003) represent the most prominent and influential theoretical framework to describe numerical cognition. It is based on cognitive and neuro-cognitive findings from brain-lesioned patients as well as functional neuroimaging which were integrated into an anatomo-functional model of number processing. It postulates three distinct and task-specific representational codes for numbers, which are subserved by distinct brain areas, and are recruited for specific functions depending on the task at hand: i) an analogue magnitude code in bilateral horizontal intraparietal sulci (hIPS), ii) a verbal code in left-hemispheric perisylvian language areas and left angular gyrus (AG), and iii) a visual Arabic number code in bilateral fusiform and lingual regions (Dehaene & Cohen, 1995; 1997; Dehaene et al., 2003).

The analogue magnitude code in bilateral hIPS is described as “a nonverbal representation of numerical quantity, perhaps analogous to a spatial map or ‘number line’” (Dehaene et al., 2003, p. 489; see blue areas in Figure 2.1). Semantic knowledge about numerical quantities, including proximity or distance between numbers (e.g., 7 is close to 8) and larger-smaller relations (e.g., 7 < 8) is entailed in this quantity system (Dehaene & Cohen, 1997). The quantity code in bilateral hIPS is suggested to provide an abstract, and thus, notation-independent representation of absolute number magnitude (but see Cohen Kadosh, Cohen Kadosh, Kaas, Henik, & Goebel, 2007). Thus, activation in this brain area is assumed to be independent of input modality or input format: the presentation of Arabic numerals, number words, or non-symbolic stimuli like dots as well as tones leads to activation in bilateral hIPS, in case one attends to the corresponding number. Thus, according to the TCM, bilateral hIPS codes the abstract meaning of numbers irrespective of modality or input format.

Furthermore, the activation in bilateral hIPS correlates with the numerical distance between two numbers in a comparison task (Arsalidou & Taylor, 2011; Pinel, Dehaene, Rivière, & Le

Bihan, 2001). On the behavioral level, the numerical distance effect reflects the finding of shorter and more accurate responses with larger numerical distance between two to-be-compared numbers (e.g., 1_8 vs. 3_4; Moyer & Landauer, 1967). Importantly, the presence of the numerical distance effect is considered to represent number magnitude processing. This indicates that bilateral hIPS seem to play a crucial role in the representation and processing of absolute magnitude of natural numbers and quantity information (Dehaene et al., 2003; Arsalidou & Taylor, 2011).

As this quantity information is assumed to be represented like on a spatially oriented number line, operating on number magnitude or performing numerical tasks requires attentional navigation along this number line. Dehaene and colleagues proposed in their extension of the TCM from 2003 that this mental orientation along the number line is subserved in bilateral posterior superior parietal lobe (PSPL; Dehaene et al., 2003; see light blue areas in Figure 2.1). Hence, the TCM assumes that bilateral hIPS is involved whenever some semantic manipulation of absolute magnitude of natural numbers is required, for example in number magnitude comparisons (Piazza, Pinel, Le Bihan, & Dehaene, 2007; Pinel et al., 2001), mental arithmetic (Arsalidou & Taylor, 2011; Chochon, Cohen, van de Moortele, & Dehaene, 1999; Pesenti, Thioux, Samson, Bruyer, & Seron, 2000), or even passive number magnitude processing (Eger, Sterzer, Russ, Giraud, & Kleinschmidt, 2003; Klein, Moeller, Nuerk, & Willmes, 2010). Additionally, orienting one's number-based attention along the mental number line while operating on number magnitude also involves bilateral PSPL (Dehaene et al., 2003).

Second, the auditory verbal code in left perisylvian language areas and left angular gyrus (AG) is associated with verbal processing of numbers (see yellow area in Figure 2.1). It comprises lexical, phonological and syntactic representations of numbers (Dehaene & Cohen, 1995, 1997). According to the TCM, it is involved in verbally-mediated processes like reading numbers aloud, understanding spoken and read number words, and the retrieval of rote learned arithmetic facts stored in long-term memory (i.e., multiplication or small addition facts).

Third, the TCM suggests that Arabic digit strings are processed in the visual Arabic number code in bilateral fusiform and lingual regions (see orange areas in Figure 2.1). Thus, these areas are dedicated to the visual recognition of Arabic digit strings (e.g., single digits, multi-digit numbers) in the visual number form area and also of number words in a left-lateralized visual word form area (Dehaene & Cohen, 1995).

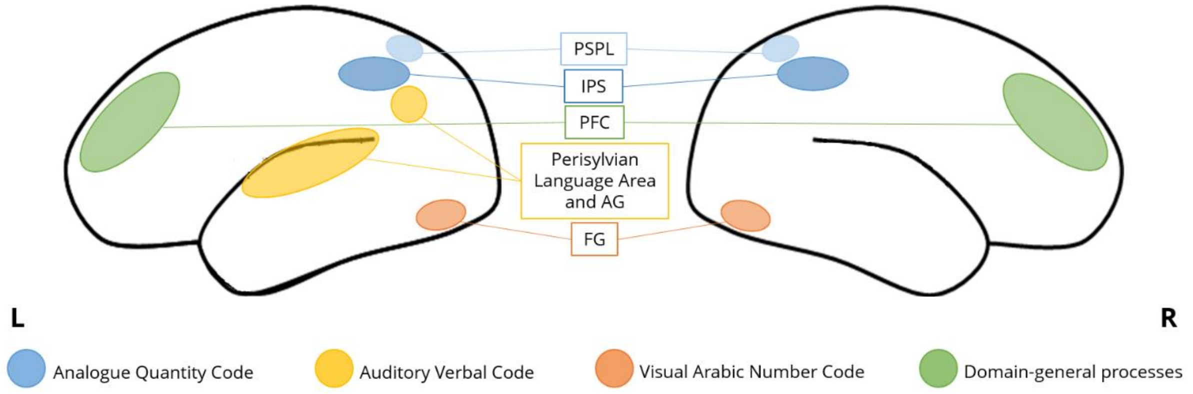

Figure 2.1: The Triple Code Model (TCM) proposed by Dehaene and Cohen (1995, 1997) and Dehaene et al. (2003). In dark blue, the bilateral intraparietal sulcus (IPS) is illustrated as hosting the analogue magnitude code. In the specification of the TCM in 2003, the posterior superior parietal lobule (PSPL), illustrated in light blue, is also described as subserving the analogue magnitude code, reflecting mental orientation along the mental number line when operating on number magnitude. In yellow, left perisylvian language areas and left AG are depicted representing the auditory verbal code. In orange, bilateral fusiform gyrus (FG) is illustrated as hosting the visual Arabic number code. The TCM assumes domain-general processes involved in number processing to be located in bilateral prefrontal cortex (PFC), depicted in green.

In sum, the TCM is the most influential theoretical framework to describe numerical cognition by integrating cognitive and neuro-cognitive data into an anatomo-functional model of number processing. However, the TCM mainly focuses on the description of domain-specific structure-function-relationships. In particular, it suggests that different aspects of numerical information (e.g., magnitude manipulations, arithmetic fact retrieval) are processed in different codes within distinct brain regions. As a consequence, it has been suggested that these representations are task-specific. For instance, number magnitude comparison is assumed to be closely linked to the number magnitude representation and, thus, to activate areas along the IPS, because these brain areas process the critical information for this task. However, for more complex tasks such as proportional reasoning, this task specificity may no longer be valid (Jacob & Nieder, 2009a, 2009b; Ischebeck et al., 2009; DeWolf et al., 2016). For instance, complex mental arithmetic has been shown to involve different and variable steps of cognitive processing, for which number specific representations are complemented by more domain-general cognitive processes such as attention, working memory, and problem solving (Ashcraft & Kirk, 2001; Imbo, Vandierendonck, & De Rammelaere, 2007). Dehaene and Cohen (1995; 1997) suggested that the specific representations of the TCM may be further supplemented by domain-general processes such as strategy choice and planning. These processes are assumed to be additionally recruited in number processing to supplement manipulating and operating on number magnitude and to be represented in (pre)frontal brain areas (Dehaene & Cohen, 1995; 1997; see green areas in Figure 2.1). However, the mechanisms and neural correlates of domain-general processes interacting with domain-specific numerical processing are still underspecified in the TCM. Similarly, the temporal dynamics of numerical processes were less in the focus of structural models like the TCM which major contribution was the description of domain-specific structure-function-relationships (but see Dehaene, 1996, for an early work on temporal processing stages in number comparisons). Yet, growing interest in temporal processing stages emphasizes the relevance of both good spatial *and* good temporal resolution to describe the processes involved in numerical cognition as (e.g., Dehaene, 1996; Pinheiro-Chagas et al., 2018; Teichmann et al., 2018; Shum et al., 2013; Hsu & Szucs, 2012; Kiefer & Dehaene, 1997).

The present thesis addresses these underspecified issues in two sections, which will be discussed in the following to serve as an outline of the individual studies. Section 1 focuses on domain-specific numerical and domain-general parietal processes involved in number processing. Section 2, for its part, focuses on the temporal course of number processing. At the end of each section, the objectives of the individual studies will be addressed.

3 Section 1: Domain-specific numerical and domain-general parietal number processing

The first section relates specifically to the parietal cortex and the assumptions the TCM makes for this specific brain region. It comprises three studies: Study 1 aims at extending the assumptions on the neural correlates for domain-specific processing of magnitude information in the analogue magnitude code to relative magnitude, Study 2 aims at investigating the involvement of parietal cortex associated with, but beyond magnitude processing, and Study 3 aims at examining the automatic association of numbers and space.

In the following, I will outline the theoretical background that led to the three research questions addressed in this section.

3.1 Extending the scope of the analogue magnitude code

The TCM proposes that bilateral hIPS hosts an analogue magnitude code in which absolute number magnitude is represented in an abstract, notation- and modality-independent way (Dehaene & Cohen, 1997; Dehaene et al., 2003). Modulation of intraparietal brain activation in accord with the numerical distance effect further substantiated this assumption, because the presence of the distance effect indicates the processing of number magnitude information (Pinel et al., 2001). Thus, absolute number magnitude seems to be represented and processed in bilateral hIPS. However, the TCM does not specifically consider other types of number magnitude such as, for instance, relative magnitude. Nevertheless, there is accumulating evidence that relative number magnitude is also processed in these brain areas. In the following, I will first outline several studies that provide additional evidence for the processing of absolute magnitude in bilateral hIPS, before going into more recent studies on the neural processing of relative magnitude.

3.1.1 Absolute number magnitude processing in bilateral hIPS

The bilateral hIPS is postulated to be the core area for the processing of and operating on absolute number magnitude in the analogue magnitude code. Previous studies showed that a fronto-parietal network including brain regions in and around the IPS is consistently associated with number processing (Amalric & Dehaene, 2018; Arsalidou & Taylor, 2011; Piazza, Pinel, Le Bihan, & Dehaene, 2007; see Nieder, 2005 for a review). Within this network, the IPS seems to be specifically involved in the processing of numerical magnitude information (Piazza et al., 2007; Pinel et al., 2001), even when magnitude processing is not explicitly required by the task at hand (Eger et al., 2003). Interestingly, activation in these specific brain areas can be modulated by the numerical distance effect. Hence, with decreasing distance between two numbers, activation in the bilateral IPS increases. This was observed for symbolic numbers and number words (Pinel et al., 2001) as well as for non-symbolic numerosities (Ansari, Dhital, & Siong, 2006; Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004). Thus, only the numerical distance, but not the notation affects the degree of activation (Pinel et a., 2001). There is accumulating evidence that bilateral IPS hosts the neural representation of number magnitude information supporting this assumption of the TCM (Dehaene & Cohen, 1995, 1997; Dehaene et al., 2003). Importantly, these findings also substantiate the notion that the analogue magnitude code seems to be notation-independent (Piazza et al., 2004).

Although the analogue magnitude code is assumed to be abstract for different modalities (i.e., visual and auditory) and notation formats (i.e., symbolic and non-symbolic), it is not specified for the magnitude information of other types of numbers like, for example, relative magnitude (e.g., magnitude of fractions, decimals, or non-symbolic proportions). Nevertheless, there is first evidence that relative magnitude is also processed in this specific brain region (DeWolf, Chiang, Bassok, Holyoak, & Monti, 2016; Ischebeck, Schocke, & Delazer, 2009; Jacob & Nieder, 2009a, 2009b).

3.1.2 Neural underpinnings of processing fractions and proportions

Several studies showed that brain areas that are typically associated with processing absolute magnitude information are also involved in processing fractions and proportions. Only recently, Lewis, Matthews, and Hubbard (2016) argued for the existence of a ratio processing system (RPS) complementary to the approximate number system (Piazza, 2010; Matthews, Lewis, & Hubbard, 2016). The RPS was found to be sensitive to non-symbolic ratio magnitude and assumed to provide a non-symbolic foundation for understanding symbolic fractions in adults (Jacob, Vallentin, & Nieder, 2012; Lewis, Matthews, & Hubbard, 201; Binzak, Matthews, & Hubbard, 2019) and in children (Kalra, Binzak, Matthews, & Hubbard, 2019).

On the neural level, Jacob and Nieder (2009a) found that bilateral IPS is involved in processing symbolic fractions independent of presentation format (i.e., fractions, e.g., ¼ vs. fraction words, e.g., a quarter). In a functional MRI adaption (fMRA) paradigm, a fraction (e.g., 1/6) was repeatedly presented. During adaptation to this specific fraction, the blood oxygen level-dependent (BOLD) signal decreased. After adaptation, participants were either presented with a deviant fraction (e.g., ½) or a fraction word (e.g., 'one-half'). The BOLD signal in bilateral IPS and bilateral prefrontal cortex recovered as a function of numerical distance between deviant and adapted fraction magnitude, irrespective of the format of the deviant. This indicated that the same populations of neurons code the same fraction magnitude, independent of the specific format. Moreover, Jacob and Nieder (2009b) observed similar intraparietal effects for non-symbolic proportions (e.g., proportions of line lengths or numerosities) with strongest effects in bilateral anterior IPS.

Importantly, the magnitude of a symbolic fraction (e.g., 1/5) might be represented by the overall numerical magnitude of the fraction as a whole (e.g., 0.2) or involve separate representations of the magnitudes of numerator and denominator. Ischebeck and colleagues (2009) were able to show that a network of activation comprising right IPS, right medial frontal gyrus, and middle occipital gyrus was modulated by overall numerical distance while brain activation was not influenced by numerator or denominator distances. Thus, proportion magnitude seems to be represented by its value as a whole, and thus, overall magnitude (Ischebeck et al., 2009; Jacob & Nieder, 2009a, 2009b). Building upon these results, DeWolf and colleagues (2016) investigated whether different symbolic numbers (i.e., fractions, integers, decimals) map onto a joint abstract magnitude code as proposed by the TCM or whether different representations exist for different number types (e.g., integers vs. symbolic proportions) or number notations (e.g., fractions vs. base-10[7]). In fact, processing fractions, integers, and decimals resulted in IPS activation as proposed by the analogue magnitude code

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[7] The base-10 place-value structure rests on the position of each digit, which determines the numerical value within the respective digit string without proportional aspects (i.e., base-10 place-value structure: e.g., 35.4 = $3 \times 10^1 + 5 \times 10^0 + 4 \times 10^{-1}$; Huber et al., 2014b).

of the TCM. However, more fine-grained multivariate analyses yielded an activation pattern for fractions distinct from decimals and integers within IPS (DeWolf et al., 2016). Thus, neural processing of proportions appeared to be sensitive to number notation (i.e., fractions vs. base-10), but not number type (integer vs. proportion).

In sum, the TCM proposes an abstract analogue magnitude code in bilateral hIPS for the processing of absolute magnitude irrespective of modality or notation. Furthermore, numerical distance modulates brain activation in bilateral hIPS, reflecting the processing of magnitude information in this brain region. Recent work also provided evidence that symbolic fractions, fraction words, and non-symbolic proportions, respectively, are processed in the same parietal areas. However, so far it has not yet been investigated systematically whether both symbolic fractions and non-symbolic proportions share an abstract neural substrate for relative magnitude processing independent of presentation format. Study 1 of the present thesis addresses this issue. For this, I aimed at investigating shared magnitude-related brain activation as modulated by overall numerical distance of symbolic and non-symbolic proportions to evaluate whether the brain regions associated with the processing of notation-independent absolute magnitude are also involved in notation-independent relative magnitude processing.

3.2 Numerical processing related to, but also beyond magnitude

The main goal of Study 1 was to answer the question whether relative magnitude information also shares an abstract neural correlate in bilateral hIPS comparable to absolute magnitude. Thus, the study focused on the domain-specific numerical aspects of relative magnitude processing on the neural level. However, other rather domain-general processes might be involved because symbolic and non-symbolic proportions require more (computational) steps than just accessing number magnitude information directly.

According to Dehaene and Cohen (1995, 1997), domain-general factors such as strategy choice and planning that influence number processing are associated with (pre)frontal brain areas. However, it was shown that the intraparietal cortex which, according to the TCM, is assumed to host a domain-specific analogue magnitude code, is also involved in a variety of sensory, motor, attention, and thus, rather domain-general functions as part of higher order (also referred to as tertiary) association cortex (Culham & Kanwisher, 2001; Humphreys & Lambon Ralph, 2015, 2017; Simon, Mangin, Cohen, Le Bihan, & Dehaene, 2002). Thus, besides domain-specific numerical processing of magnitude information, the IPS is also associated with complex and multimodal domain-general cognitive functions *beyond* magnitude processing in a wide range of sensory, motor, and attention functions. In particular, it has been found to be involved in a variety of visuospatial tasks such as grasping, hand reaching, attention orienting, spatial working memory, saccades, mental rotation as well as guidance of actions (Culham & Kanwisher, 2001; Simon et al., 2002). These cognitive functions partly involve domain-general processes and thus show partly overlapping activation in parietal cortex, while smaller sub-regions show domain-specific numerical activations (Humphreys & Lambon Ralph, 2015).

Focusing more specifically on the IPS and the superior parietal lobule (SPL), these brain regions are activated by various tasks including calculation, top-down attention, phonological tasks, executive semantics and tool-praxis decisions (Humphreys & Lambon Ralph, 2015). Moreover, IPS and SPL are specifically associated with the storage and manipulation of items held in working memory during executively demanding and goal-directed tasks (Humphreys & Lambon Ralph, 2015; Jonides et al., 1998). Furthermore, IPS is involved in response-selection processes (Göbel, Johansen-Berg, Behrens, & Rushworth, 2004) and the suppression of task-irrelevant distractors (Wojciulik & Kanwisher, 1999). Because of these non-automatic and goal-directed processes, it was assumed that IPS and SPL support a general top-down processing system as part of a fronto-parietal executive system across domains (Cabeza, 2008; Corbetta & Shulman, 2002; Humphreys & Lambon Ralph, 2015, 2017).

Thus, processes that are subserved in the parietal cortex are not exclusively domain-specific number magnitude processing itself, but rather are associated with or necessary for the processing of numbers such as top-down attention, spatial representation, working memory, eye movements, and the guidance of actions (Culham & Kanwisher, 2001; Humphreys & Lambon Ralph, 2015). This is in line with the idea that the IPS hosts a domain-general multi-demand system associated with a variety of cognitive processes, ranging from attentional processes to mental navigation as well as from pointing and grasping to number processing (e.g., Duncan, 2010; Fedorenko et al., 2013; Humphreys & Lambon Ralph, 2015, 2017; Simon et al., 2002).

Importantly, there is accumulating evidence that different goal-directed processes interact as they all require this domain-general multi-demand system (e.g., Duncan, 2010; Fedorenko et al., 2013; Hubbard, Piazza, Pinel, & Dehaene, 2005; Humphreys & Lambon Ralph, 2015). For instance, Knops and colleagues (2009) found that the same areas that are involved in spatial attention also contribute to mental arithmetic. Furthermore, overlapping activation was also observed with mental calculation, language, and saccades in the left posterior segment of the IPS (Simon et al., 2002). These results support the assumption that number processing co-opts parietal circuits involved in sensorimotor tasks such as saccades and spatial attention, and importantly, also shares brain regions with other higher cognitive functions such as language.

To sum up, as part of the tertiary association cortex the parietal cortex is not only associated with domain-specific numerical processes, but also with a wide range of sensory, motor, and attention functions. As these different cognitive functions also share common features of executive demands, it can be assumed that the IPS is not a brain region specifically dedicated to domain-specific numerical processing (Humphreys & Lambon Ralph, 2017). Rather, the ability to process numbers and numerosities seems to involve number-unspecific processes such as top-down control processes, spatial attention, working memory, as well as executive processes which are hosted in an intraparietal executive system across domains with more domain-specific areas surrounding it (Humphreys & Lambon Ralph, 2017).

Nevertheless, these domain-general processes might be involved in operating on magnitude information. However, so far it has not yet been investigated whether there is a shared neural correlate for number processing in the intraparietal cortex *beyond* overall magnitude processing. Study 2 of this thesis will address this question by investigating shared domain-specific numerical and domain-general aspects of proportion processing in the bilateral IPS. In particular, Study 2 reports on complementary aspects of the same dataset as Study 1 of the current thesis. While Study 1 focused on magnitude-specific processing of proportions as reflected by the numerical distance effect, Study 2 rather addresses complementary domain-general processes involved in proportion processing beyond overall magnitude.

3.3 Automatic association of numbers and space

As reviewed above, parietal activation associated with number processing seems to reflect both domain-specific numerical and domain-general cognitive processes. This is in line with the neuronal recycling hypothesis, which proposes that more recent cultural inventions such as reading and arithmetic co-opt evolutionarily older brain areas and inherit their structural constraints (Dehaene & Cohen, 2007; Barkow et al., 1992). In particular, number processing and mental arithmetic seem to share at least some parietal circuits with visuospatial tasks including eye-movements, grasping, pointing, attentional processes, and mental navigation (Humphreys & Lambon Ralph, 2015, 2017; Knops et al., 2009; Simon et al., 2002). Importantly, although those cultural inventions “invade” cortical areas of evolutionarily older functions, “their prior organization is never entirely erased” (Dehaene & Cohen, 2007, p. 384).

This is also in line with another influential neurocognitive model, the ATOM theory (A Theory of Magnitude; Walsh et al., 2003), which assumes that numbers and space are jointly processed and represented in the inferior parietal and prefrontal cortex by a generalized magnitude system. In particular, the ATOM theory proposes that the domains of number and space share this magnitude system based on the same metric (e.g., magnitude/extension), because in both domains items can be quantified, estimated, or compared (Cipora, Patro, & Nuerk, 2015; Walsh, 2003). Thus, following the ATOM theory and the neural recycling hypothesis, (visuo-)spatial processes might enhance or interfere with number processing whenever number magnitude is processed.

Overlapping structures of number and visuospatial processing seem to form the neural basis for the metaphor of a spatially oriented mental number line. According to the TCM, number magnitude is represented on this spatially oriented mental number line by the analogue magnitude code. On the neural level, spatial orientation of the mental number line is supposed to be reflected by activation in PSPL, a region associated with attentional navigation (Dehaene et al., 2003). This region seems to be automatically engaged when attending to specific quantities on the number line. Thus, the association of numbers and space should be automatic (but see van Dijck & Fias, 2011 for an alternative hypothesis). In fact, this can be observed on the behavioral level. Even when number magnitude is irrelevant for the task at hand (e.g., in parity judgment tasks), small numbers are responded to faster with the left and large numbers with the right hand (i.e., Spatial-Numerical Associations of Response Codes (SNARC) effect; Dehaene et al., 1993; see Wood et al., 2008 for a review and meta-analysis). In the following, the concept of spatial-numerical associations will be introduced briefly.

3.3.1 Spatial-numerical associations

Spatial-numerical associations (henceforth SNAs) like the SNARC-effect reflect the spatial dimension of the representation of number magnitude. As such, the SNARC basically led to the common metaphor of the mental number line to describe the mental representation of number magnitude. In recent years accumulating evidence has been provided that various kinds of numerical concepts can be associated with a spatial dimension. Thus, SNAs were found amongst others for non-symbolic numerosities (e.g., de Hevia, Girelli, Addabbo, & Cassia, 2014; de Hevia, Veggiotti, Streri, & Bonn, 2017; Patro & Haman, 2012), symbolic numbers (e.g., Dehaene, Bossini, & Giraux, 1993; Wood, Willmes, Nuerk, & Fischer, 2008), operation signs (e.g., Pinhas, Shaki, & Fischer, 2014), mental arithmetic (e.g., Klein, Huber, & Nuerk, 2014; Pinhas & Fischer, 2008), number line estimation (e.g., de Hevia & Spelke, 2010), and line bisection (e.g., de Hevia & Spelke, 2009). However, these SNAs have long been viewed as one big melting pot without any further differentiation. Lately, however, a distinction between extension and direction was proposed (Cipora et al., 2015; Cipora, Schroeder, Soltanlou, & Nuerk, in press; Patro, Nuerk, Cress, & Haman, 2014). For extensions, numerical magnitude is associated with spatial extensions, such as numerosity-length matching (de Hevia & Spelke, 2010), extension of abstract rules across different spatial-numerical dimensions (Lourenco & Longo, 2010) or line bisection (de Hevia & Spelke, 2009). For directions, numerical magnitude is associated with a specific spatial direction. Thus, larger numbers are usually associated with right in horizontal direction (Dehaene et al., 1993) or up in vertical direction (Ito & Hatta, 2004). In the following, I will focus on recent literature specifically on directional SNAs and their development in particular.

3.3.2 Development of SNAs

In the following, I illustrate the development of SNAs for different types of numerical concepts, starting with SNAs in non-symbolic numerosities, followed by symbolic numbers and operation signs, and the place-value structure as part of directional SNAs.

3.3.2.1 Directional SNAs for non-symbolic numerosities

Long before children start going to school, they develop SNAs for non-symbolic numerosities. In particular, already at the age of seven months, infants prefer numerosities increasing from left to right as compared to right to left (de Hevia et al., 2014). Moreover, the visual presentation of non-symbolic numerical cues sufficed to induce attentional shifts to a specific side in space in eight- to nine-month-old infants. Infants were faster at detecting targets on the right following a larger cue and targets on the left following a smaller numerosity (Bulf, de Hevia, & Macchi Cassia, 2015). This indicates that SNAs for non-symbolic numerosities exist already very early in life. Because SNAs occurred even before children entered formal education or acquired number symbols, Bulf and colleagues (2015) concluded that the mental number line “is not merely a product of human invention” (p.6). However, whether early (or animal) SNAs are conclusive for an innateness assumption has been a matter of intense recent debate (Núñez & Fias, 2017; Patro & Nuerk, 2017; Rugani, Betti, Ceccarini, & Sartori, 2017; Rugani, Vallortigara, Priftis, & Regolin, 2015), because also other origins such as cultural mechanisms have been proposed (Nuerk et al., 2015). Thus, during early childhood SNAs might also develop through cultural and social experiences such as monitoring adult reading behavior, pretending to read or to write, attentional-directional preferences, and direct spatial-numerical learning (Nuerk et al., 2015; Patro, Fischer, Nuerk, Cress, 2015).

3.3.2.2 Directional SNAs for symbolic numbers

With increasing age, children associate numerosities and numerical magnitudes in general to symbolic digits. Importantly, there is accumulating evidence for SNAs in symbolic numbers. The most prominent finding is the aforementioned SNARC-effect: in Western cultures, where writing is from left to right, small numbers are responded to faster with the left hand relative to the right hand and larger numbers faster with the right hand relative to the left even when number magnitude was irrelevant for the task at hand (e.g., in parity judgements: Dehaene et al., 1993; Fischer, Castel, Dodd, & Pratt, 2003; Wood et al., 2008). It was argued that this effect originates from a left-to-right oriented mental number line resulting in faster responses when response side and position of the respective number on the mental number line are congruent (i.e., left – small and right – large; Dehaene et al., 1993; Gibson & Maurer, 2016).

The first study on the SNARC effect for symbolic numbers in children used a parity judgment task and found that only children from grade 3 onwards showed a significant symbolic SNARC effect (Berch, Foley, Hill, & McDonough Ryan, 1999; see also van Galen & Reitsma, 2008). However, White and colleagues (2012) observed a significant symbolic SNARC effect based on parity judgments already in second graders (mean age: 7.5 years; for similar results in a magnitude-relevant task, see also Gibson and Maurer, 2016). Interestingly, Hoffmann and colleagues (2013) found a SNARC-like effect already in 5.8-year-old children. In an adapted digit color judgment task, children had to indicate the color of a centrally presented number (e.g., red or green) with either their left or their right hand. Children implicitly responded faster with their left hand to smaller numbers and with their right hand to larger numbers. Thus, in adapted tasks Western children exhibit SNARC-like effects already at 5.8 years of age (Hoffmann, Hornung, Martin, & Schiltz, 2013), whereas the classical SNARC effect based on parity judgments can only be observed from grade 2 onwards (Berch et al., 1999; White et al., 2012). However, in Chinese children who receive mathematical instructions earlier, a symbolic SNARC effect for the standard parity judgment task was observed already at an age of 5 years (Yang, Chen, Zhou, Xu, & Dong, 2014). Hence, these children already developed automatic directional SNAs for symbolic numbers at this early age, which might be due to their longer experience with symbolic numbers (Yang et al., 2014; Zhou et al., 2007). Thus, with increasing age and experience, SNAs were found to become stronger with children exhibiting robust directional SNAs for symbolic numbers at an age of 7 years (at least in

Western children; White et al., 2012) and already earlier in children who received earlier mathematical instructions (Yang et al., 2014).

3.3.2.3 Directional SNAs for operation signs

Interestingly, directional SNAs are not limited to processing non-symbolic numerosities or symbolic numbers. Instead, also the mere presentation of an arithmetic operation sign (e.g., + or –) can lead to spatial associations. This effect is termed operation sign space association (OSSA) effect (Pinhas et al., 2014). The OSSA effect describes the finding that adults respond faster with their left hand when presented with a minus sign, and faster with their right hand when presented with a plus sign (Pinhas et al., 2014; Cipora et al., in press). They seem to automatically direct their attention along the mental number line towards the operation indicated by the respective operation sign: to the left when subtracting and to the right when adding (for an alternative explanation see Proctor & Cho, 2006).

This directional SNA for operation signs can also be observed on the neural level. Mathieu and colleagues (2017) found that the mere perception of a plus sign elicited more pronounced neural activation in brain regions associated with spatial attention shifting (e.g., frontal eye fields, PSPL) than the perception of a multiplication sign in adults. In contrast to this, in children rather the right hippocampus seemed to contribute to the association between operation signs and space in children (Mathieu et al., 2018). This brain area was shown to be associated with spatial representations and navigation (Burgess, Maguire, & O'Keefe, 2002; Maguire et al., 1998). Interestingly, activation in right hippocampus increased with increasing age. This indicated that children build a representation of arithmetic operations in mental space with increasing age and experience (Mathieu et al., 2018). During development a shift from hippocampal to fronto-parietal activation for operation signs seems to take place indicating increasing automation with increasing age and experience (Mathieu et al., 2017, 2018).

3.3.2.4 Place-value structure as part of directional SNAs

Another category of directional SNAs relates to the processing of multi-digit numbers because the value of a digit is defined inherently by its spatial position in the digit string (Cipora et al., in press). Thus, when processing multi-digit numbers, the correct value must be assigned to the respective digit based on its spatial position in the base-10 place-value structure. For multi-digit numbers, it was shown that adults process individual digits separately, but in parallel as indicated by the unit-decade compatibility effect (e.g., compatible trials: 79 vs. 23, 7 > 2 and 9 > 3; incompatible trials: 38 vs. 64, 3 < 6, but 8 > 4; Moeller, Fischer, Nuerk, &

Willmes, 2009a; Nuerk, Weger, & Willmes, 2001). In incompatible trials, the magnitude of the unit-digits interferes and, in turn, leads to slower responses although the comparison of the decade-digits would suffice to choose the larger number. Interestingly, the compatibility effect increased with age and experience possibly due to more parallel and automated processing (Mann, Moeller, Pixner, Kaufmann, & Nuerk, 2011). While 2nd graders who just learned about multi-digit numbers, processed them sequentially from left to right starting at the leftmost digit pair (e.g., tens; Nuerk, Kaufmann, Zoppoth, & Willmes, 2004), 3rd and 4th graders showed both sequential and parallel processing, and thus, a mixed sequential and parallel processing mode (Nuerk et al., 2004; Mann et al., 2011). With increasing experience, 5th graders finally showed a more adult-like parallel processing of multi-digit numbers (Nuerk et al., 2004). Importantly, the spatial position in a number is not only decisive for digits in the base-10 place-value structure, but also for specific symbols such as polarity signs (e.g., 3 vs. -3) or the decimal point (e.g., 2.74 < 27.4). Thus, not only the position of a digit, but also the position of a specific symbol determines the value of a number. For such multi-symbol numbers, it is assumed that the respective symbol, for instance the polarity sign, is processed in a similar way as an individual digit in a multi-digit number, because comparable interference effects were observed (Huber, Cornelsen, Moeller, & Nuerk, 2014; but see Ganor-Stern, Pinhas, Kallai, & Tzelgov, 2010; Shaki & Petrusic, 2005; Varma & Schwartz, 2011 for alternative explanations). Although comparing the polarity signs would suffice to choose the larger number, the decade-digit interfered in incompatible trails (e.g., -86 vs. +42; – < +, but 8 > 4), leading to slower responses compared to compatible trials (e.g., -42 vs. +86). Thus, multi-symbol numbers seem to be processed in the same parallel way as multi-digit numbers in adults. Importantly, the mental number line seems to extend to the left for negative numbers in adults (Fischer, 2003). However, negative numbers might be processed less automatically compared to positive numbers and, in turn, induce weaker SNAs (Fischer & Rottmann, 2005; Nuerk & Willmes, 2004).

Taken together, the TCM posits that number magnitude is represented on a spatially oriented mental number line in ascending order from left to right. On the neural level, it can be observed that PSPL, a region typically involved in attentional navigation, is automatically engaged when attending to numerical magnitude. Interestingly, even when numerical magnitude is irrelevant for the task at hand, numerical magnitude and space are automatically asociated (e.g., SNARC). Such spatial associations for numbers develop already very early in life for non-symbolic numerosities. With increasing age and experience, children link numerical magnitudes to symbolic digits showing significant SNARC effects from 7 years of age (in Western cultures). Subsequently, SNAs also develop for arithmetic operation signs. However, this has only been investigated on the neural level in children so far. In adults, the mental number line is extended to the left, because multi-symbol numbers such as negative numbers also induce spatial associations.

So far, however, there is no study investigating developmental aspects of multi-symbol number processing in children, who were just introduced to this numerical concept in school. Thus, it is not clear yet, whether the association of numbers and space is automatic, even when a specific number concept has just been acquired. Study 3 of the present thesis addressed this issue. In this study, I aimed at investigating how automatically different aspects of multi-symbol numbers (e.g., magnitude, polarity sign, place-value integration) are associated with space even when the specific number concept (i.e., negative numbers) has just been acquired.

3.4 Objectives of Section 1

Section 1 of this thesis aims at qualifying the assumptions of the TCM for the parietal cortex and for processes subserved by this specific brain region by investigating domain-specific numerical and domain-general parietal aspects of number processing. On the one hand, this approach served to extend the scope of the analogue magnitude code as the representation for absolute magnitude information. On the other hand, rather domain-general influences in number processing related to, but beyond overall magnitude processing were examined on the neural and the behavioral level. In the following, the objectives of each of the three studies of Section 1 will be made in paragraphs (a) – (c).

(a) According to the TCM, absolute magnitude is processed in the bilateral hIPS (Dehaene and Cohen, 1995, 1997; Dehaene et al., 2003). In Study 1, I aimed at evaluating the role of the bilateral hIPS in relative magnitude processing. Therefore, I investigated whether the bilateral hIPS is not only involved in processing absolute, but also relative magnitude information. More specifically, Study 1 examined whether there is a shared, notation-independent domain-specific neural correlate for the processing of relative magnitude information. To pursue this issue, I employed symbolic (e.g., fractions and decimals) and non-symbolic proportions (e.g., proportional dot patterns and pie charts) in an fMRI study using magnitude comparison tasks. In particular, I was interested in the shared neural activation observed for magnitude processing of symbolic and non-symbolic proportions. As an indicator for magnitude processing, the distance was modulated on the neural level. Thereby, I was able to investigate whether relative magnitude information is represented in similar brain regions as typically associated with absolute magnitude processing, and thus, whether the analogue magnitude code proposed by the TCM can be extended to relative magnitude.

(b) The TCM proposes that domain-general processes such as planning and strategy choice, which are additionally involved in number processing and required for manipulating and operating on number magnitude, are represented in prefrontal brain areas (Dehaene and Cohen, 1995, 1997; Dehaene et al., 2003). However, as shown above, IPS is also associated with domain-general cognitive functions *beyond* processing overall number magnitude, in addition to domain-specific processing of magnitude information. These domain-general parietal processes might be involved when operating on magnitude information. Therefore, in Study 2 I aimed at investigating whether there is a shared neural correlate for proportion processing in the intraparietal cortex *beyond* overall magnitude processing. To pursue this issue, Study 2 reports on complementary aspects of the same dataset as Study 1. Thus, I again employed symbolic and non-symbolic proportions with a different scope (domain-specific magnitude processing in Study 1, domain-general processes in proportion processing beyond overall magnitude in Study 2). Processing proportions is specifically suited for this purpose as their processing requires several (computational) steps which involve domain-general processes in addition to processing number magnitude information. To this end, I chose a three-step procedure. In a first step, I used a univariate conjunction analysis (Nichols, Brett, Andersson, Wager, & Poline, 2005) on the whole-brain level to identify the location of shared neural correlates of proportion processing beyond overall magnitude. In a second step, I particularly investigated the mechanisms involved in part-whole processing, by contrasting the activation found for bipartite part-whole relations (i.e., fractions, dot patterns, and pie charts) with decimals, because processing of part-whole relations specifically requires the integration of the two parts, which is associated with more domain-general cognitive processes like putting into relation. Furthermore, the mere presence of a shared neural correlate does not necessarily imply a shared underlying neural process (Cohen Kadosh et al., 2005; Pinel, Piazza, Le Bihan, & Dehaene, 2004). Therefore, in a third step, a multivariate representational similarity analysis (RSA; Kriegeskorte, Mur, & Bandettini, 2008) within the shared neural correlate found in the bilateral IPS was employed to further differentiate the similarity of the intraparietal BOLD response for symbolic and non-symbolic proportions. In doing so, I was able to evaluate whether symbolic (e.g., fractions and decimals) and non-symbolic proportions (e.g., pie charts and dot patterns) share an underlying neural process.

(c) According to the TCM, number magnitude is represented on a spatially oriented mental number line (Dehaene et al., 2003). On the neural level, the association between numbers and space is reflected by activation in PSPL, an area associated with attentional navigation, which seems to be automatically engaged when attending to number magnitude. On the behavioral level, this automatic association is reflected by faster response latencies to number magnitude with a specific side in space (e.g., small – left, large – right), even if number magnitude is irrelevant for the task at hand (Dehaene et al., 1993; Wood et al., 2008). In Study 3 of my thesis, I aimed at investigating whether the association between magnitude and space is given also for numerical concepts (e.g., negative numbers) that are just acquired. This is of particular interest, as it was shown that SNAs get stronger with age and experience (Ninaus et al., 2017). Thus, I was interested in how automatically different aspects of numbers (e.g., magnitude, polarity sign, place-value integration) are associated with space in 6th graders, who just learned about multi-symbol numbers (e.g., positive and negative numbers) in school. Therefore, I examined directional spatial-numerical associations reflected by SNARC-like digit-direction and OSSA-like sign-direction congruency effects as well as the sign-digit compatibility effect (Huber et al., 2014) when 6th graders performed magnitude comparisons with positive and negative numbers.

4 Section 2: The temporal dynamics of number processing

Section 2 addresses the temporal dynamics of number processing, for which the TCM does not make any suggestions. In fact, the focus of the TCM did not lie on the description of temporal dynamics of number processing. Rather, its goal was to indicate structure-function-relationships on the neural level based on empirical evidence from experimental psychological studies, neuropsychological patients, and neurofunctional imaging. Neurofunctional imaging data provide relatively precise spatial but low temporal resolution, so it is hardly suitable for mapping the temporal dynamics of cognitive processes. Nevertheless, Dehaene (1996) recognized the relevance of temporal aspects of numerical cognition early on as he investigated the temporal dynamics of the number comparison task by means of ERPs. Only recently the interest in temporal aspects of numerical cognition increased (e.g., Pinheiro-Chagas et al., 2018; Teichmann et al., 2018; Kiefer & Dehaene, 1997; Hsu & Szucs, 2012; Shum et al., 2013; Daitch et al., 2016) highlighting the benefit of good temporal resolution to adequately understand the complex processes involved in numerical cognition.

In fact, there are methods to capture and understand temporal dynamics of cognitive processing. In research on language processing, EEG and ERPs are often used to gain information about the underlying temporal dynamics (e.g., Friederici, 2002; Friederici, Gunter, Hahne, & Mauth, 2004; Hahne & Friederici, 1999; Leonard et al., 2010; Meyer, Obleser, Kiebel, & Friederici, 2012; Opitz, Mecklinger, Friederici, & Cramon, 1999). In this context, reading research also highlighted the particular value of the eye-tracking methodology to better understand the temporal dynamics during reading (Calvo & Meseguer, 2002; Deutsch et al., 2003; Joseph et al., 2008; Just & Carpenter, 1980; Rayner, 1998; Rayner & Pollatsek, 1989). Eye-tracking provides a complementary approach to investigate the temporal aspects of the underlying cognitive processes. Importantly, by means of certain eye-tracking measures early and late cognitive processes can be distinguished to draw conclusions about the time course of underlying cognitive processes (e.g., Just & Carpenter, 1980; Rayner & Pollatsek, 1989). However, these techniques have been used less often and less systematically in numerical cognition research to disentangle the temporal dynamics of different numerical processes. Nevertheless, measuring eye-fixation behavior while operating on numbers (e.g., number comparison, arithmetic problems) can provide valuable information for understanding the underlying cognitive processes, because on-line monitoring of these processes is enabled. In the following, I will shortly introduce recent research on the temporal processing stages of number processing and mental arithmetic using EEG, ERPs, MEG, and ECoG before going more into detail on the differentiation between early and late processing stages by means of eye-tracking and a first model on the temporal dynamics in the number bisection task.

4.1 Research on temporal processing stages in number processing using EEG, MEG, and ECoG

In recent years, the interest in investigating the temporal processing stages in numerical cognition by means of non-invasive and invasive neuro-cognitive methods increased, because EEG, MEG, and ECoG in particular have a very high temporal resolution in the range of milliseconds. A first study was already published in 1996 by Dehaene, who examined the temporal processing stages of the number comparison task using ERPs and the additive-factors method (Sternberg, 1969). Dehaene (1996) identified several stages in the number comparison task. Visual features are processed early in right posterior regions before a left-lateralized (for number words) or a bilateral (for Arabic digits) early negativity at around 100-150 msec reflected notation-specific identification processes and stimulus comprehension.

Numerical distance was found to affect ERPs in right-lateralized parieto-occipito-temporal regions arising at 170 to190 msec irrespective of notation (number words or digits; see also Hsu & Szucs, 2012). This was followed by a major central positivity reflecting non-specific motor preparation. An error-related negativity in prefrontal regions was observed after an erroneous response was given indicating error processing (Dehaene, 1996). In another ERP study by Kiefer and Dehaene (1997) simple and difficult single-digit multiplication problems were examined. Simple multiplication problems were processed rapidly in left parietal areas indicating the fast retrieval of arithmetic facts, whereas difficult multiplication problems required longer processing in parietal regions of both hemispheres reflecting the computation of the result for more difficult problems (Kiefer & Dehaene, 1997; for an overview on arithmetic strategies, see Hinault & Lemaire, 2016).

Only recently has the interest in the temporal aspects of number processing been rekindled again. Teichmann and colleagues (2018) showed that magnitude information of digits is accessed slightly earlier compared to dice. This delay between the two notations could be attributed to a difference in conversion speed into an abstract magnitude representation as proposed by the TCM because of the relative frequency and familiarity of the stimuli (Teichmann et al., 2018). In mental arithmetic, a cascade of partially overlapping processing stages was observed (Pinheiro-Chagas et al., 2018). Pinheiro-Chagas and colleagues (2018) applied machine learning techniques to MEG signals to decompose different processing stages in mental addition and subtraction. They were able to decode the first operand based on its visual properties, while the decoding of the second operand rested on both visual and magnitude information. Furthermore, during the presentation of the second operand the classifier trained on discriminating subtractions versus additions cross-generalized and distinguished between smaller versus larger numbers reflecting calculation and manipulation of quantities along a number line (Pinheiro-Chagas et al., 2018). At the decision stage, fast and overlapping processing stages for identifying the proposed result, judging its correctness, and pressing the response button were observed. MEG topographies showed that in line with previous research the evoked responses evolved over time from posterior to anterior sensors both after each stimulus onset and across the entire trial (Pinheiro-Chagas et al., 2018; Dehaene, 1996).

Combined spatial-temporal processing was recently investigated by means of ECoG. Daitch and colleagues (2016) revealed early visual processing in the visual number form (VNF) area and the posterior inferior temporal gyrus (pITG). Neurons in these brain regions responded selectively to the visual presentation of individual numbers. Later processes engaged in carrying out arithmetic computations were found in subregions of the IPS similar to parietal areas involved in numerosity tuning (Harvey et al., 2013; Piazza et al., 2004). Additionally, more posterior sites in IPS were involved in domain-general and less-selective responses (Daitch et al., 2016).

4.2 Differentiation between early and late processing stages by means of eye-tracking

The eye-tracking methodology offers a complementary approach to investigate the temporal aspects of the underlying cognitive processes. First, it was applied in the field of reading research with a strong focus on saccades (i.e., fast discontinuous movements of the eyes). It was found that the sensitivity to visual input is reduced during saccades and saccades are programmed in parallel with comprehension processes during reading (e.g., Dearborn, 1906; Dockeray & Pillsbury, 1910; Erdmann & Dodge, 1898). With increasing sensitivity of eye-tracking devices, the underlying processes involved in reading and other higher cognitive tasks, such as scene perception and visual attention, were examined (for a review, see Rayner, 1998). Quickly it became clear that distinct eye-tracking measures allowed for the differential evaluation of underlying cognitive processes. On the one hand, first fixation duration (i.e., the time of the first fixation on a stimulus) and gaze duration (i.e., aggregated duration of consecutive fixations on the same stimulus) were shown to be sensitive to early stimulus-driven aspects such as frequency of words (Rayner, Ashby, Pollatsek, & Reichle, 2004; Liversedge & Findlay, 2000; for an overview, see Rayner & Pollatsek, 1989). On the other hand, the overall number of fixations but also total reading time on a specific stimulus were argued to reflect later top-down mediated processes such as the duration of plausibility checks and judgments (Deutsch et al., 2003; Joseph et al., 2008).

Just and Carpenter (1980) developed a processing model of reading comprehension specifically based on gaze durations (see Figure 4.1). The model proposed that gaze durations reflect the time to execute comprehension processes. Thus, longer fixations indicate longer times needed to comprehend a stimulus. This claim is based on two assumptions: the immediacy and the eye-mind assumption. These assumptions suggest that the location of an eye-fixation reflects the spatial locus (i.e., immediacy assumption: what is processed at the moment), while the duration of a fixation indicates the time course of cognitive processing (i.e., eye-mind assumption: how long it takes to process the information at the fixated position, e.g., Just & Carpenter, 1980; Rayner & Pollatsek, 1989; for a critical view see Irwin, 2004).

The model by Just and Carpenter (1980) illustrates processes during reading. In the column on the left, the processing stages during reading are depicted in their usual sequence of execution. The influence of working memory during reading is represented in the middle column, mediating knowledge stored in long-term memory and ongoing comprehension processes during reading. The column on the right illustrates information stored in long-term memory and procedural knowledge on the execution of reading sequences (Just & Carpenter, 1980).

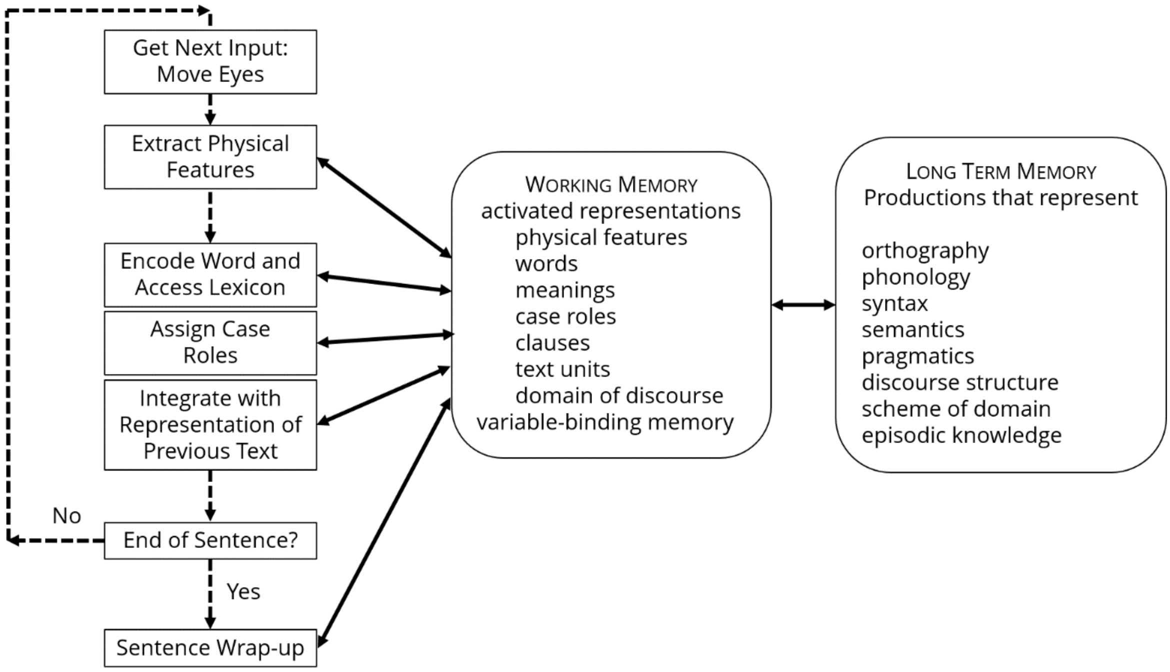

Figure 4.1. Early model for the major processes and structures in reading comprehension adapted from Just and Carpenter (1980, p. 331). Solid lines indicate data-flow paths, while dashed lines denote canonical flow of control.

The first processing stage during reading (i.e., get next input, move eyes) is the starting point to find information, encoding and processing it. The duration of the whole process depends on the goal of the reader. When a reader only skims a text, the goals are achieved much faster than when a text needs to be learned by heart. As soon as the goal for processing a specific word is satisfied, the resulting action is “get next input” (Just and Carpenter, 1980).

During the encoding process, it is assumed that physical features are extracted first. Thus, the printed word is parsed into its visual features. These features are stored in working memory for further processing. Afterwards, the mental lexicon is accessed. Here the representation of the word is activated, and its concept is transferred into working memory. Frequently used words or words that have appeared earlier in the text have a high base level of activation and are, in turn, accessed faster than infrequent words. In this way, the model can account for frequency and repetition effects (Just & Carpenter, 1980).

In the next step, relations among words (e.g., agent, recipient, location, time, action, or instrument) are determined. This is achieved by heuristics which consider word meaning together with semantic and syntactic context information. The output is a representation of the semantic role of the word with respect to the other constituents of the sentence or the paragraph (Just & Carpenter, 1980).

Afterwards, the sentence read must be related to prior knowledge either acquired from the text or retrieved from long-term memory to capture the coherence of the text. Thus, new aspects have to be integrated into older, already existing information. As each new word is read, the representation is updated integrating the new information. This immediate interpretation might, however, lead to hasty decisions, for instance, in case of ambiguous words. Misinterpretations are often detected when new information is inconsistent with prior knowledge. In this case, the reader returns directly to the locus of misinterpretation for re-evaluation.

Finally, at the sentence wrap-up stage any inconsistencies that could not be resolved within the sentence are handled. This involves searching for referents that have not been assigned yet as well as constructing relations between sentences to match the overall context held in working memory or stored in long term memory.

In sum, this model describes the processing stages during sentence reading from word encoding to integrating and relating new information to prior knowledge based on eye-tracking data. This clearly reflects the added value of evaluating eye-fixation behavior as it allows for an online and more in-depth investigation of the underlying cognitive processes. Importantly, the assumptions based on eye-tracking measures in reading research can easily be transferred to research in other content domains such as numerical cognition.

In the following, I will introduce a model for the temporal dynamics in the number bisection task based on eye-tracking measures to describe early and late processing stages.

4.3 A first model on the temporal dynamics of the number bisection task

A study by Moeller and colleagues (2009b) used advantages of the eye-tracking technique to examine the temporal dynamics of performing the number bisection task. In the number bisection task, participants have to evaluate whether the middle number of a triplet corresponds to the arithmetic integer mean of the given interval (e.g., 3_5_7) or not (e.g., 3_4_7). Two specific aspects of numbers, among others, can be used to solve this problem:

parity information and multiplicativity. Only when the two outer numbers are of the same parity, an integer mean of the triplet exists (e.g., 21_25_29 vs. 21_25_28, correct mean would be 24.5). Furthermore, multiplicativity indicates whether a triplet is part of a multiplication table or not (e.g., 21_24_27 vs. 21_25_29). In multiplicatively related triplets the decision is facilitated by the automatic activation of multiplication fact knowledge (Nuerk, Geppert, van Herten, & Willmes, 2002). To evaluate the time course of processes involved in the number bisection task, distinct eye-tracking measures were considered, which allow to distinguish between early bottom-up and later top-down mediated processes. Gaze duration was examined to reflect early stimulus-driven aspects while total reading time revealed rather later top-down processes. In line with the assumption that multiplicativity should activate automatic bottom-up influences of multiplication fact knowledge, the authors observed multiplicatively related triplets were classified faster than unrelated ones. On the other hand, an influence of the parity manipulation was found in total reading times. Responses to bisectable triplets were slower than those to non-bisectable triplets indicating a facilitatory effect of parity inhomogeneity between the two outer numbers of non-bisectable triplets. Bisectability as reflected by the same parity of the two outer numbers reliably prolonged total reading times indicating the integration of information across numbers, magnitude manipulation, and the verification of rules (Moeller, Fischer, Nuerk, & Willmes, 2009b). Based on this differentiation, Moeller and colleagues (2009b) developed a model specifying the processing stages of the number bisection task (see Figure 4.2).

The model was adapted from the early reading model by Just and Carpenter (1980; cf. Figure 4.1). It distinguishes between an early stimulus-driven bottom-up processing stage impacting on gaze duration and later rather top-down mediated processes influencing total reading time. At the initial processing stage, the single digits of the two-digit numbers are identified and assigned their stimulus-driven lexical values (e.g., place-value position, magnitude, and multiplicativity). Thus, the physical features of the digits of a certain number are extracted first, which activates the visual number form. Second, the digits are integrated into the place-value structure of the Arabic number system so that number semantics can be assigned, and thus, number magnitude can be accessed. Afterwards, specific attributes implicated in multiplication fact knowledge are mapped to the number (e.g., element of a (specific) multiplication table, parity information). Subsequently, the number is put into relation with any preceding number. This procedure is repeated until all numbers of the triplet are encoded. Importantly, it is assumed that these so far mentioned processing stages operate largely automatically (Henik & Tzelgov, 1982; Moeller, Fischer, et al., 2009b; Rusconi, Galfano, Speriani, & Umiltà, 2004). Thus, multiplicativity is processed already at this early processing stage when specific attributes are attached to the number. In fact, Moeller and colleagues (2009b) observed this early processing of multiplicativity in their gaze duration measures, which are assumed to reflect early stimulus-driven processes (e.g., Calvo & Meseguer, 2002). Finally, at a wrap-up stage, potential rules are applied to the encoded number (triplet) and plausibility of the internally computed result is checked. As this processing stage requires the representation of the whole triplet, these processes capture rather late processing stages as reflected by total reading time (e.g., Joseph et al., 2008). Afterwards, the final decision is made, and a response is given.

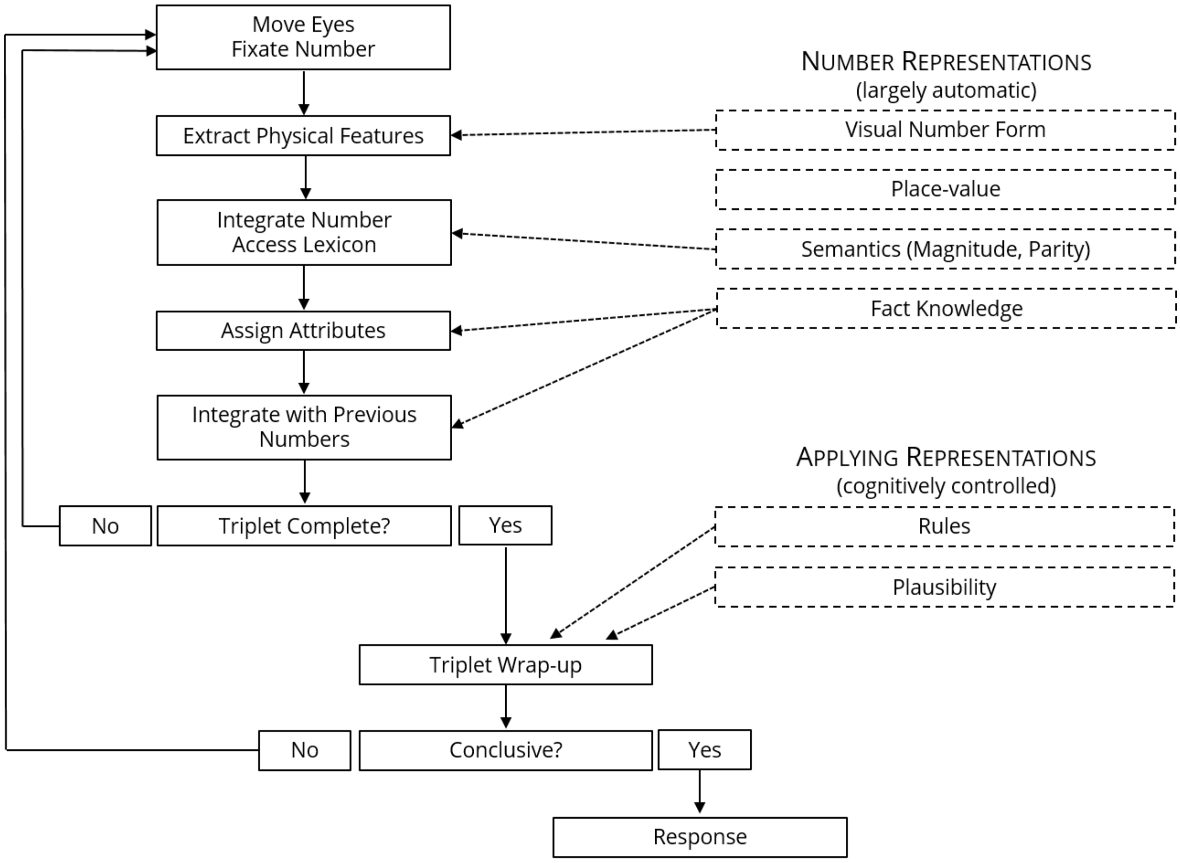

Figure 4.2. Processing model of eye fixation behavior in the number bisection task adapted from Moeller et al. (2009b, p. 215). The full line boxes on the left connected with full arrows reflect the processing stages of the model while the dashed line boxes on the right represent the different representations of numerical information involved at the different processing stages. Dashed arrows indicate at which processing stage the involvement of the respective representation is assumed (Moeller et al., 2009b).

Importantly, the model of Moeller and colleagues (2009b) does not only describe the temporal sequence of dynamics of the number bisection task. Rather, it may be used to explain eye fixation behavior in other numerical and arithmetic tasks. First, the problem size effect (i.e., processing time increases with increasing number magnitude) is reflected in gaze duration:

Brysbaert (1995) found increasing gaze duration as number magnitude increases indicating that number magnitude is automatically activated during number processing. This is also in line with the model of Moeller and colleagues (2009b).

Second, addition problems requiring a carry operation demand the application of rules. A carry operation is needed, whenever the sum of the digits in one position of a number is equal or larger than 10. For instance, for 47 + 35 the sum of the units is 12 (i.e., 7 + 5). Thus, the decade digit of the unit sum 12 (i.e., 1) has to be added to the sum of the decade digits of the addends (i.e., 4 + 3 + 1 = 8). This operation requires the application of a rule. According to the model, applying rules should be reflected by measures indicating later top-down processes such as total reading time or total number of fixations in a specific area of the visual stimulus. In fact, total reading time upon the unit digits of the summands was found to increase when a carry operation is needed (Moeller, Klein, & Nuerk, 2011b). This indicates the involvement of later top-down mediated processes when applying rules during carry operations in addition problems.

Taken together, eye-tracking seems to offer possibilities to differentiate between early and late processing stages in cognitive processes such as reading or number processing. In fact, reading research exploited these possibilities to differentiate between distinct cognitive mechanisms in a fine-grained manner by means of eye-tracking for decades. Since the 1980s, it has been generally valid in reading research that measures such as first fixation and gaze duration on a stimulus reflect early stimulus-driven and thus bottom-up mechanisms, whereas the overall number of fixations and total reading time on the same stimulus are associated with later top-down mediated processes (e.g., Inhoff, 1984, 1985; Calvo & Meseguer, 2002; Deutsch et al., 2003; Joseph et al., 2008). However, so far, such a distinction between bottom-up and top-down mechanisms has only been used to a limited extent in numerical cognition research. Nevertheless, the number of studies using eye-tracking as a method increased steadily over the last years, emphasizing the relevance of the results and findings from eye-tracking for our understanding of numerical cognition (for a short review, see Hartmann, 2015).

4.4 Objectives of Section 2

Based on neuropsychological and neurofunctional data, the TCM provides relatively good spatial resolution postulating structure-function-relationships in the human brain. Unfortunately, these data do not provide good temporal resolution during number processing. In recent years, the relevance of studying temporal aspects of number processing and mental arithmetic was emphasized using EEG, ERPs, MEG, and ECoG (e.g., Dehaene, 1996; Kiefer & Dehaene, 1997; Pinheiros-Chagas et al., 2018; Teichmann et al., 2018; Shum et al., 2013) to more comprehensively account for the complex cognitive processes and mechanisms involved in numerical cognition. Eye-tracking provides a complementary approach to investigate the temporal aspects of the underlying cognitive processes. Reading research highlighted the benefits of employing different eye-tracking measures to distinguish between early and late processing stages. Yet, these techniques were used less often and less systematically in numerical cognition research to identify the cognitive processes involved in number processing. Moeller and colleagues (2009b) proposed a model on the temporal dynamics in the number bisection task based on eye-tracking data. In Study 4 of this thesis, a comprehensive review and discussion of empirical eye-tracking studies in numerical cognition from the last 40 years is conducted. In particular, I was interested in aspects of the temporal dynamics of the processes involved in numerical cognition. Therefore, I aimed at subdividing the underlying cognitive processes into early, stimulus-driven bottom-up mechanisms and later, rather cognitively controlled top-down processes by means of different eye-tracking measures. Furthermore, besides domain-specific aspects of number processing, attention was also paid to the influence of domain-general processes on number processing and vice versa. Finally, these findings were summarized in an extension of the model proposed by Moeller and colleagues (2009b). While the model by Moeller et al (2009b) was based on number bisection data only, the model extension presented in Study 4 aims at enriching the model by Moeller and colleagues (2009b) with the findings from the review on temporal aspects from numerous different tasks to obtain improved generalizability of the temporal aspects in numerical cognition.

5 Research aims driving the studies enclosed

The aim of the present thesis is to evaluate domain-specific numerical and domain-general contributions to number processing, which have not yet been specified in the TCM. Particularly, I focus on two major goals: specifying the assumptions the TCM makes about domain-specific numerical and domain-general parietal processes involved in number processing (principally independent from temporal aspects and time-critical methods) and extending the scope of the TCM by enriching the model with early bottom-up and later top-down mediated processing stages (based on findings of time-critical methods). In the following, the research aims driving the enclosed studies are presented, before the individual studies addressing these issues will be presented in detail. Subsequently, the research questions are put into perspective in the General Discussion section. Then, the results of the studies are discussed with respect to the overall objective of the present thesis: a first attempt to complement neurofunctional correlates of domain-specific numerical and domain-general processes with aspects of temporal dynamics of number processing.

(a) In Study 1, I examined whether relative magnitude information shares an abstract, notation-independent domain-specific neural correlate comparable to absolute magnitude processing in the analogue magnitude code of the TCM.

(b) In Study 2, I investigated whether there is also a shared neural correlate for rather domain-general processes related to, but beyond overall magnitude processing in proportion processing in the parietal cortex as the TCM associated domain-general processes with frontal brain regions. Based on this, I evaluated whether symbolic and non-symbolic proportions also share an underlying neural process.

(c) In Study 3, I explored how automatically different aspects of numbers (e.g., magnitude, polarity sign, place-value integration) are associated with space in 6th graders as the TCM proposed that the processing of number magnitude is automatically associated with spatially moving along the mental number line.

(d) In Study 4, I evaluated aspects of temporal dynamics of the processes involved in numerical cognition by means of eye-tracking as temporal processing stages of the processes involved in number processing were less in the focus of the TCM. In doing so, I distinguished between early, stimulus-driven bottom-up mechanisms and later, rather cognitively controlled top-down processes involved in number processing.

PART II: EMPIRICAL STUDIES

Studies of Section 1:

Domain-specific numerical and domain-general parietal number processing

Study 1: Mock, J., Huber, S., Bloechle, J., Dietrich, J.F., Bahnmueller, J., Rennig, J., Klein, E., & Moeller, K. (2018). Magnitude processing of symbolic and non-symbolic proportions: an fMRI study. *Behavioral and Brain Functions,* 14:9.

Study 2: Mock, J., Huber, S., Bloechle, J., Bahnmueller, J., Moeller, K., & Klein, E. (2019). Processing symbolic and non-symbolic proportions: Domain-specific numerical and domain-general processes in intraparietal cortex. *Brain Research, 1714*, 133-146.

Study 3: Mock, J., Huber, S., Cress, U., Nuerk, H.-C., & Moeller, K. (2019). Negative numbers are not yet automatically associated with space in 6th graders. *Journal of Cognition and Development, 20(4),* 611-633.

6 Study 1: Magnitude processing of symbolic and non-symbolic proportions: an fMRI study[8]

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Abstract

Background: Recent research indicates that processing proportion magnitude is associated with activation in the intraparietal sulcus. Thus, brain areas associated with the processing of numbers (i.e., absolute magnitude) were activated during processing symbolic fractions as well as non-symbolic proportions. Here, we investigated systematically the cognitive processing of symbolic (e.g., fractions and decimals) and non-symbolic proportions (e.g., dot patterns and pie charts) in a two-stage procedure. First, we investigated relative magnitude-related activations of proportion processing. Second, we evaluated whether symbolic and non-symbolic proportions share common neural substrates.

Methods: We conducted an fMRI study using magnitude comparison tasks with symbolic and non-symbolic proportions, respectively. As an indicator for magnitude-related processing of proportions, the distance effect was evaluated.

Results: A conjunction analysis indicated joint activation of specific occipito-parietal areas including right intraparietal sulcus (IPS) during proportion magnitude processing. More specifically, results indicate that the IPS, which is commonly associated with absolute magnitude processing, is involved in processing relative magnitude information as well, irrespective of symbolic or non-symbolic presentation format. However, we also found distinct activation patterns for the magnitude processing of the different presentation formats.

Conclusion: Our findings suggest that processing for the separate presentation formats is not only associated with magnitude manipulations in the IPS, but also increasing demands on executive functions and strategy use associated with frontal brain regions as well as visual attention and encoding in occipital regions. Thus, the magnitude processing of proportions may not exclusively reflect processing of number magnitude information but also rather domain-general processes.

6.1 Background

Fractions, ratios, and proportions are among the most ubiquitous forms of numerical information encountered in everyday life. Yet, they are also one of the most difficult concepts to learn and even adults frequently fail to process them correctly (Gigerenzer, 2002; Siegler, Fazio, Bailey, & Zhou, 2013). Therefore, understanding the processing and acquisition of fractions and proportions poses one of the most challenging problems in numerical cognition research as well as mathematics education (NMAP, 2008).

In teaching and learning fractions, symbolic and non-symbolic presentation formats are often presented side by side to successfully foster conceptual understanding of proportional relations (Gabriel et al., 2012; Rau, Aleven, & Rummel, 2015; Rau, Aleven, Rummel, & Rohrbach, 2012). The present study aims at exploring why these pedagogic approaches might be successful from a neurocognitive perspective. To this end, we aimed at broadening the understanding of mechanisms underlying proportion processing by investigating the neural correlates of processing symbolic fractions and non-symbolic proportions in the human brain. In particular, a shared neural correlate for the magnitude processing of fractions and proportions, independent of their presentation format, might explain the efficacy of these pedagogic approaches.

Before the details of the current study will be outlined, we will give a brief summary of recent advances in numerical cognition research by describing (i) neural networks involved in number processing in general, (ii) processes of symbolic and non-symbolic quantities and their underlying neural correlates in particular, and (iii) argue how our investigation of a common neural substrate for both symbolic and non-symbolic proportion processing can be informative for a better understanding of relative magnitude processing.

Neural networks involved in number processing

Previous studies on number processing showed that the intraparietal sulcus (IPS) is crucially involved in the processing of absolute quantity and number magnitude (Dehaene, Piazza, Pinel, & Cohen, 2003; Nieder, 2005; Piazza, Pinel, Le Bihan, & Dehaene, 2007; Pinel, Dehaene, Rivière, & Le Bihan, 2001). To evaluate the processing of magnitude information conveyed by natural numbers and fractions, the numerical distance effect in magnitude comparison tasks has been employed repeatedly. The numerical distance effect reflects the finding of shorter and more accurate responses with larger numerical distance between two to-be-compared numbers (e.g., 1_9 vs. 4_5; Moyer & Landauer, 1967).

Importantly, the presence of the numerical distance effect is considered to indicate number magnitude processing in the task at hand (Meert, Grégoire, & Noël, 2009; Moyer & Landauer, 1967).

Behavioral results on the distance effect were substantiated by findings showing that activation within the IPS was negatively correlated with numerical distance in number magnitude comparison tasks for natural numbers (e.g., Arsalidou & Taylor, 2011, but see Bugden, Price, McLean, & Ansari, 2012). This indicates that the IPS seems to play a crucial role in the representation and processing of number magnitude information (Arsalidou & Taylor, 2011; Bugden et al., 2012; Jolles et al., 2016; Menon, Rivera, White, Glover, & Reiss, 2000; Pinel, Piazza, Le Bihan, & Dehaene, 2004).

However, although neuroimaging research on number processing primarily focused on parietal cortex and especially on the IPS, a rather complex system of functional brain networks was observed to contribute to numerical cognition in general (Fias, Menon, & Szucs, 2013; Menon, 2015). Besides the IPS, numerical distance was also shown to negatively correlate with activation in bilateral prefrontal and precentral cortex, indicating fronto-parietal networks of number magnitude processing (Ansari, Garcia, Lucas, Hamon, & Dhital, 2005; Pinel et al., 2001). However, recent research suggests an even broader network to be involved in numerical cognition.

For instance, there is evidence that early perceptual numerical features are decoded in the ventral visual stream, including V1 and the inferior temporal cortex (ITC), before visual-spatial features of numerical quantity are processed in the IPS and the superior parietal lobule (SPL; Ansari, 2008; Fias et al., 2013). Moreover, it was suggested that a widespread fronto-parietal network, comprising IPS, supramarginal gyrus, supplementary motor areas, and dorsolateral prefrontal cortex (DLPFC), is involved in planning, executing, and monitoring arithmetic procedures as well as maintaining intermediate results (Dijck, Gevers, & Fias, 2009; Fias et al., 2013; Hitch, 1978; Majerus et al., 2010). Additionally, DLPFC as well as anterior cingulate cortex (ACC) were also associated with processes of cognitive control to optimize performance by monitoring and adapting task execution as well as inhibiting undesired responses (Ansari, Grabner, Koschutnig, Reishofer, & Ebner, 2011; Cohen Kadosh et al., 2005; Fias et al., 2013; Kaufmann et al., 2005). Furthermore, the angular gyrus (AG) was also argued to be involved in verbal retrieval of math facts (Dehaene et al., 2003; Dehaene, Spelke, Pinel, Stanescu, & Tsivkin, 1999; Grabner et al., 2009, but see Bloechle et al., 2016; Jolles et al., 2016). Finally, the anterior insula and ventrolateral prefrontal cortex were suggested to be involved in processes of guiding and maintaining goal-directed attention (Fias et al., 2013; Menon, 2015).

Thus, although parietal regions, and in particular the IPS, play a central role in numerical cognition, there is growing evidence that cognitive processes such as working memory, cognitive control, and executive functions associated with frontal, temporal, and insular cortex are also vital to access numerical information, employ representations of numerical knowledge, and manipulate quantities during calculations.

Neural processing of symbolic numbers and non-symbolic quantities

While the IPS is thought to comprise a notation-independent representation of the magnitude information conveyed by numerals (Ansari et al., 2005; Chochon, Cohen, van de Moortele, & Dehaene, 1999), words (Dehaene, 1996; Pinel et al., 2001), or non-symbolic arrays as quantities (Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004; Venkatraman, Ansari, & Chee, 2005), Sokolowski and colleagues (Sokolowski, Fias, Mousa, & Ansari, 2017) observed several additional areas jointly activated in processing symbolic as well as non-symbolic quantities. As a result of a meta-analysis, the authors reported joint activation of bilateral inferior parietal lobule (IPL) and precuneus as well as left superior parietal lobule (SPL) and right superior frontal gyrus (SFG) during the processing of both symbolic and non-symbolic numbers. Furthermore, Holloway and colleagues (Holloway, Price, & Ansari, 2010) reported a right-sided dominance of joint processing of symbolic and non-symbolic magnitude in right IPL and SPL. Several other studies also indicated that this region is involved in processing symbolic (Ansari et al., 2005; Chochon et al., 1999; Eger, Sterzer, Russ, Giraud, & Kleinschmidt, 2003; Pinel et al., 2001) and non-symbolic numerical magnitude (Ansari, Dhital, & Siong, 2006; Piazza et al., 2004, 2007). Furthermore, Holloway and colleagues (Holloway et al., 2010) found joint activations for symbolic and non-symbolic magnitude in the inferior frontal gyrus (IFG) extending to middle frontal gyrus, right anterior insula, ACC, and SFG. Thereby, these findings imply that these brain regions comprise format-independent processing of symbolic and non-symbolic magnitudes.

However, recent research also indicated that symbolic and non-symbolic magnitudes are processed by both overlapping but also distinct neural systems (Holloway et al., 2010; Piazza et al., 2007; Sokolowski et al., 2017). The processing of non-symbolic magnitude was observed to involve visual cortex areas due to greater visual demands such as the individuation and summation of non-symbolic items (Holloway et al., 2010). The meta-analysis of Sokolowski and colleagues (Sokolowski et al., 2017) revealed a right-lateralized fronto-parietal network including right SPL, IPL, precuneus, SFG, and insula as well as middle occipital gyrus involved in non-symbolic number processing compared to symbolic numbers.

In contrast, stronger activation for processing symbolic compared to non-symbolic numbers was found in right supramarginal gyrus, IPL, and left AG. Holloway and colleagues (Holloway et al., 2010) also reported involvement of left AG as well as superior temporal gyrus during symbolic compared to non-symbolic number processing. These regions have repeatedly been reported to be important during exact calculation (Dehaene et al., 1999; Venkatraman et al., 2005) and arithmetic fact retrieval (Delazer et al., 2005; Grabner et al., 2009).

Thus, previous research suggests that the human brain seems to represent numerical magnitude both format-dependent as well as format-independent, and thus, abstract (Sokolowski et al., 2017).

Neural correlates of processing symbolic fractions and non-symbolic proportions

Recent studies indicated that the same brain regions associated with processing absolute magnitude are also involved in processing fractions and proportions, and thus, relative magnitude in general (Ischebeck et al., 2010; Ischebeck, Schocke, & Delazer, 2009; Jacob & Nieder, 2009a, 2009b). Importantly, the magnitude of a fraction (e.g., ¼) might be represented by the numerical magnitude of the fraction as a whole (e.g., 0.25) or involve separate representations of the magnitudes of numerator and denominator. Ischebeck and colleagues (2009) found that activation within the right IPS, right medial frontal gyrus, and middle occipital gyrus was only modulated by the overall numerical distance between fractions and was not influenced by numerator or denominator distances. Therefore, these authors concluded that fraction magnitude is represented holistically at the neural level.

Moreover, Jacob and Nieder (2009a) provided evidence that the processing of fraction magnitude within the IPS seems to be independent of presentation format. Using a functional MRI adaptation (fMRA) paradigm, participants were habituated to a given fraction number (e.g., $^1/_6$) and were then presented with either a deviant fraction number (e.g., ½) or fraction word (e.g., 'one-half'). During adaptation, the blood oxygen level-dependent (BOLD) signal decreased. When presented with deviants, signal in bilateral IPS, bilateral prefrontal cortex, and a small cluster in the right cingulate cortex recovered as a function of numerical distance between deviant and adapted fraction magnitude. This effect was independent of presentation format. This suggests that the same populations of neurons seem to code the same fraction magnitude, irrespective of presentation format.

Jacob and Nieder (2009b) also observed that the BOLD signal in bilateral IPS and lateral prefrontal cortex decreased during the adaptation phase in an fMRA experiment using non-symbolic proportions (e.g., proportions of line lengths or numerosities). Again, BOLD signal recovered when presented with a deviant stimulus as a function of the distance between the deviant and the adapted proportion with strongest effects in bilateral anterior IPS. Further clusters of activations were found in bilateral prefrontal and precentral regions with seemingly right-lateralized dominance.

Taken together, previous work indicates that a network comprising bilateral IPS, prefrontal cortex, middle occipital gyrus, and cingulate cortex, which was reported to be activated for processing absolute numerical magnitude, is also activated when relative magnitude needs to be processed, irrespective of presentation format.

The present study

So far, a common neural substrate for processing proportion magnitude was observed only for i) symbolic fractions and fraction words (Jacob & Nieder, 2009a), ii) proportional line lengths and non-symbolic numerosities (Jacob & Nieder, 2009b), and iii) different pairs of symbolic fractions (e.g., same denominator: 2/7 vs. 5/7; same nominator: 3/5 vs. 3/8; mixed pairs: 2/3 vs. 1/5; Ischebeck et al., 2009). Thus, it has not yet been investigated systematically whether both symbolic and non-symbolic proportions have a common neural substrate for relative magnitude processing reflected by shared activation for processing relative magnitude independent of presentation format. However, this is an important question: in teaching and learning settings, symbolic and non-symbolic presentation formats of fractions and proportions are often used side by side to introduce and foster the understanding of proportional relations. To allow for a better and easier-to-grasp conceptual understanding of proportionality aspects, symbolic fractions in particular are often presented and illustrated using non-symbolic pie charts and proportional dot patterns (Matthews & Chesney, 2015; Rau, Aleven, & Rummel, 2009, 2013, Rau et al., 2015, 2012; Siegler, Fuchs, Jordan, Gersten, & Ochsendorf, 2015). Additionally, understanding of fraction magnitude is usually supported by references to its respective equivalent in decimal notations (Common Core State Standards Initiative, 2010). Furthermore, non-symbolic proportions can be displayed either discretely involving countable units such as patterns of, for instance, blue and yellow dots or continuously without segmentation as in pie charts to support the conceptual understanding of fractions. Therefore, the current study aimed at investigating whether magnitude processing of symbolic and non-symbolic proportions has a common neural substrate. We conducted an fMRI study using magnitude comparison tasks with symbolic (e.g., fractions and decimals) and non-symbolic proportions (e.g., dot patterns and pie charts), respectively.

As an indicator of magnitude-related processing, we specifically considered the numerical distance effect in our analyses. In a two-stage procedure, we first evaluated distance-related activations in proportion processing in different formats before addressing the issue of a common neural substrate underlying both symbolic and non-symbolic proportion processing.

Because of the similarity of decimals to integers, we expected activation in areas typically associated with the processing of symbolic numbers for the processing of decimals. These areas involve bilateral IPS, left AG, and supramarginal gyrus (Ansari, 2008; Holloway et al., 2010; Sokolowski et al., 2017). Additional to activations in bilateral IPS, we expected stronger frontal activations in SMA, DLPFC, and ACC for the processing of fraction magnitude due to higher cognitive and working memory demands reflecting additional computations necessary for accessing fraction magnitude (Cohen Kadosh et al., 2005; Fias et al., 2013; Ischebeck et al., 2009; Kaufmann et al., 2005). For proportions reflected by dot patterns, comparable cognitive and working memory demands were expected, and thus, activations in frontal areas such as DLPFC and ACC in addition to IPS (Jacob & Nieder, 2009b). Furthermore, we hypothesized that dot patterns should elicit stronger activations in visual-occipital areas because of higher visual demands as well as right IPS due to their non-symbolic nature (Ansari et al., 2006; Holloway et al., 2010; Piazza et al., 2004, 2007). For pie charts, we expected activations in a fronto-parietal network including SMA, DLPFC and IPS as well as in occipital brain regions due to necessary visual processing and evaluations of part-whole relations as well as the resulting working memory demands.

As all previous studies on processing fractions or non-symbolic proportions showed an involvement of bilateral intraparietal cortex with a right-lateralized preference as well as activations in PFC, we also expected to find joint magnitude-related fronto-parietal activation in bilateral IPS and PFC for all four presentation formats.

6.2 Materials and Methods

Participants

Twenty-four right-handed volunteers (13 female, mean age = 23.2 years; *SD* = 2.99 years) participated in the study. All participants were university students. After being informed about the experimental procedure, they gave their written consent in accordance with the protocol of the local Ethics Committee of the Medical Faculty of the University of Tuebingen. All participants reported normal or corrected to normal vision and no previous history of neurological or psychiatric disorders. They received monetary compensation for their participation.

Design and Procedure

We employed a block design with alternating comparison task blocks in four conditions (i.e., fraction, decimal, pie chart, dot pattern comparison tasks). Blocks were presented in pseudo-random order. In total, we ran 24 blocks (six blocks per condition) consisting of one practice trial and four critical trials each. Thus, the experiment consisted of six practice and 24 experimental trials per condition (24 practice and 96 experimental trials in total). Each task block was built as follows: at the beginning of each block, a cue indicating the upcoming proportion type for the next five trials was presented for 500ms. Subsequently, a black screen was presented for 4,000ms. The cue was the fraction 1/4 shown in the different presentation formats in the center of the screen against grey background. Afterwards, critical trials were presented starting with a black fixation cross against grey background for 500ms, followed by the presentation of a proportion stimulus for up to 5,000ms. Participants had to respond within this time limit by pressing one of two MRI compatible response buttons with either their left (indicating left proportion larger) or right thumb (indicating right proportion larger). When participants responded faster than the given 5,000ms, a mask was presented in the remaining time (visual noise consisting of blue, yellow, and grey pixels). Then the next trial was presented. The procedure of the beginning of a block is shown in Figure 6.1. There was no jitter between successive stimuli. At the end of each block, a black screen was shown for 6,000ms.

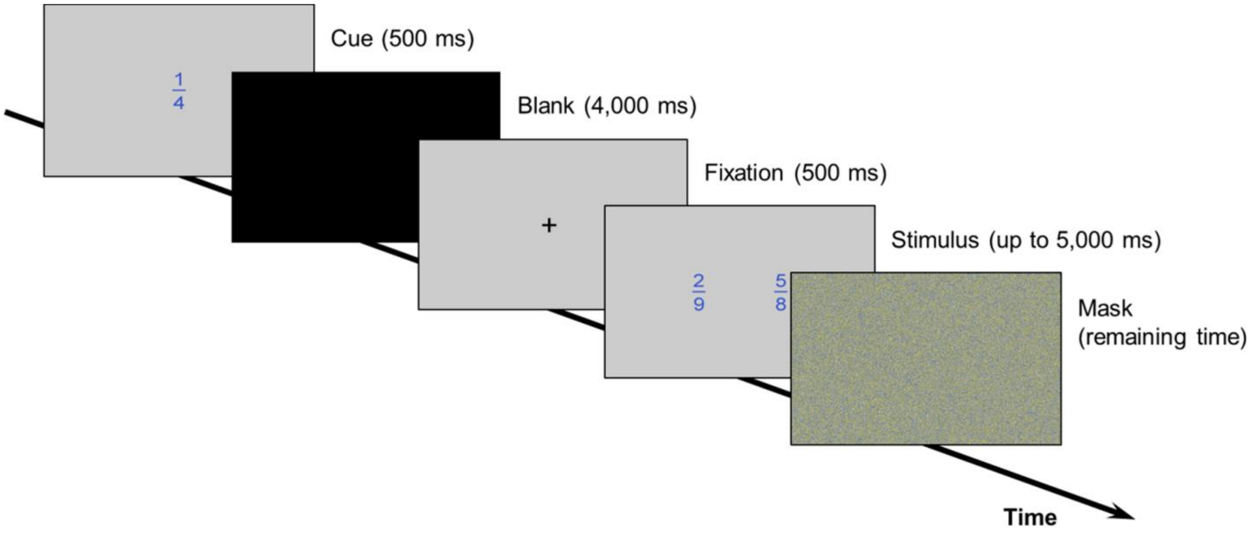


Figure 6.1: Illustration of the experimental procedure at the beginning of each block (i.e., one out of five trials).

Stimuli

We applied four different presentation formats of proportions: fractions, decimals, pie charts, and dot patterns (see Figure 6.2). For each of these four presentation formats, we constructed 30 items. Proportions were presented in pairs with the magnitude of the first proportion ranging from 0.13 to 0.86 and of the second proportion ranging from 0.22 to 0.89. Absolute distances between proportions ranged from 0.02 to 0.69.

We first generated the symbolic fraction items and converted them into the other presentation formats. Numerators of the fractions ranged from 1 to 8 and denominators from 2 to 9. Fractions were constructed such that in half of the items the comparison of numerators and denominators was either congruent or incongruent with the comparison of overall fraction magnitude. In this context, congruency means that separate comparisons of numerator and denominator magnitudes yielded the same answer as the comparison of the overall magnitudes of fraction pairs (e.g., $1/5 < 2/9$ with $1 < 2$ and $5 < 9$). In incongruent pairs, separate comparisons of numerator and denominator magnitudes yielded opposing answers as compared to the overall magnitude of the fractions (e.g., $5/9 < 2/3$, but $5 > 2$ and $9 > 3$). Hence, participants could not solve the task correctly, when relying on the magnitude of numerators or denominators only. In the next step, we constructed decimals by dividing numerators by denominators and rounding up the result to two digits after the decimal mark. Fractions as well as decimals were presented in blue (RGB-values: 53, 85, 204; font type: Arial; font size: 80) on a grey background (RGB-values: 204, 204, 204). One proportion was located on the left half (x/y-coordinates: 356 / 384 px), whereas the other one was located on the right half (x/y-coordinates: 668 / 384 px) of the screen (screen resolution: 1024 × 768 px).

Pie charts were drawn by dividing circles into two pie segments according to the magnitude of the respective fraction items. For instance, 5/9 was drawn by coloring 5/9 of the pie in blue (same blue as for fractions) and 4/9 in yellow (RGB-values: 203, 187, 0). The same grey as for fractions and decimals was used as a background color. Moreover, the location of the yellow part varied pseudo-randomly. We varied the size of the circles such that in half of the items the larger proportion was also larger according to the visual area of the blue pie segment, whereas in the other half of the items it was smaller. Thereby, we ensured that participants could not select the larger proportion by relying only on the visual area of pie segments. The diameter of pies ranged from 95 px to 289 px.

Dot patterns were drawn on an invisible rectangular area of size 491 × 363 px in the center of the left and the right side of the screen. Location of dots was varied randomly in these invisible rectangular areas. Diameter of dots varied randomly from 21 px to 98 px. Dot patterns were colored according to the fractions they denoted using the same colors as for pie charts. For instance, the dot pattern of 5/9 was drawn by coloring 5 dots in blue and 4 dots in yellow (and thus, 5 out of 9 dots were colored in blue). Moreover, we equated the sum of the yellow and blue areas of the dots across the two dot patterns which had to be compared to ensure that participants could not rely on visual area when comparing the dot patterns.

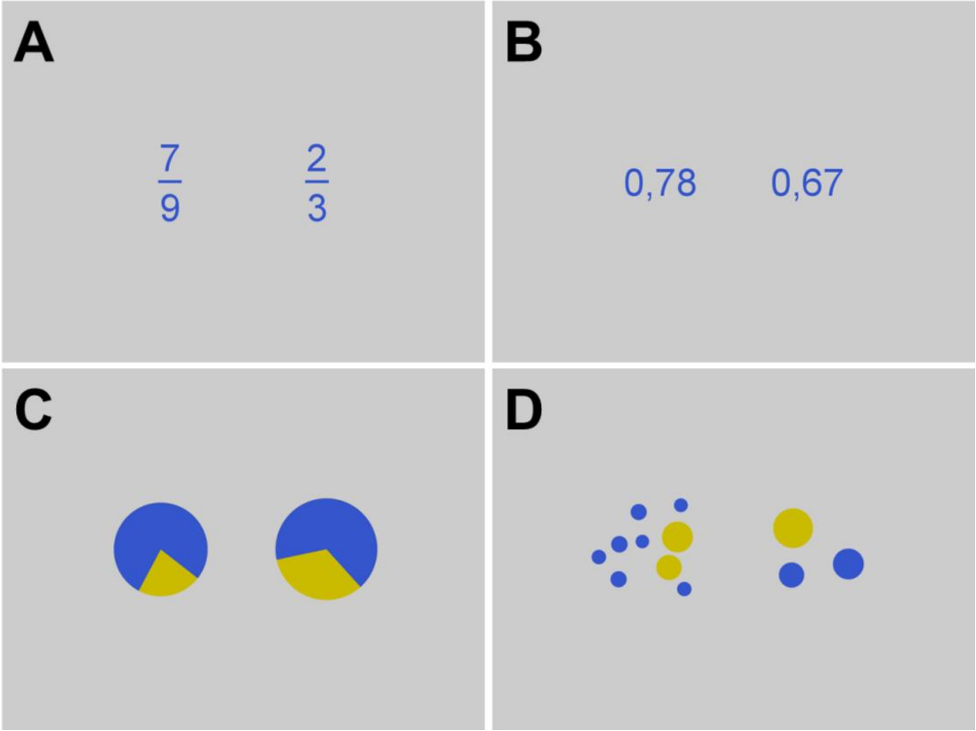


Figure 6.2: Example stimuli (7/9 vs. 2/3) for the four different presentation formats. A depicts fractions, B decimals, C pie charts and D dot patterns.

fMRI data acquisition

MRI data were acquired using a 3T Siemens Magnetom TrioTim MRI system (Siemens AG, Erlangen, Germany). A high resolution T1-weighted anatomical scan (TR = 2300 s, matrix = 256 × 256, 176 slices, voxel size = 1.0 × 1.0 × 1.0 mm^3; FOV = 256 mm², TE = 2.92 ms; flip angle = 8°) was collected at the end of the experimental session. All functional measurements covered the whole brain using standard echo-planar-imaging (EPI) sequences (TR = 2400 ms; TE = 30 ms; flip angle = 80°; FOV = 220 mm², 88 x 88 matrix; 42 slices, voxel size = 2.5 × 2.5 × 3.0 mm^3, gap = 10%).

FMRI data was acquired in a single run. Total scanning time was approximately 20 minutes. We included pauses between blocks in which a black screen was presented for 6,000 ms.

Behavioral data analysis

We analyzed both reaction times and accuracy. A first inspection of the distribution of reaction times showed that they were strongly skewed to the right. To approach normal distribution while conserving statistical power, we used the inverse transformation and transformed reaction times into speed with measurement unit 1/sec (Ratcliff, 1993).

We analyzed speed by running a linear mixed effects model (LME) and accuracy by running a generalized linear mixed model (GLME) with logit as link function and assuming a binomial error distribution. We ran (G)LME instead of analysis of variances (ANOVA) to be able to include random effects for both, participants and items to take into account that besides drawing only a sample of participants, we also included only a sample of all possible items (Baayen, Davidson, & Bates, 2008). Moreover, running ANOVA on accuracy (or error data) can result in spurious effects (Jaeger, 2008). In the LME, we included fixed effects of condition (fractions, decimals, pie charts, and dot patterns) and distance between proportions as well as their interaction, random intercepts for participants as well as items (crossed random effects), and a random slope for condition (i.e., a maximal model; (Barr, Levy, Scheepers, & Tily, 2013)). In the GLME, we included the same fixed effects and random intercepts for participants and items. Moreover, we effect-coded the predictor condition and centered the continuous predictor distance.

We considered only correctly solved trials in the analysis of speed. Additionally, we removed trials with absolute z-scaled residuals of the full model larger than ±3. In total, we considered 82.6% of all trials for the analysis of speed.

Statistical analyses were run using R (R Core Team, 2015) and the R package lme4 for running (G)LME (Bates, Maechler, Bolker, & Walker, 2015). *P*-values for fixed effects of LME were calculated running *F*-Tests using the Kenward-Roger approximation for degrees of freedom (Judd, Westfall, & Kenny, 2012). For GLME, we ran likelihood ratio tests (LRT). These methods are available via the R package afex (Singmann, Bolker, & Westfall, 2015). Post-hoc tests were run using the R package multcomp (Hothorn, Bretz, & Westfall, 2008) and corrected for multiple testing using the false discovery rate procedure by Benjamini and Hochberg (Benjamini & Hochberg, 1995).

fMRI data analysis

fMRI data analysis was performed using SPM12 (http://www.fil.ion.ucl.ac.uk/spm). Images were slice-time corrected, motion corrected, and realigned to each participant's mean image. Motion parameters did not exceed 2.5 mm translation in total (i.e., they did not exceed voxel size) and a head rotation of

1.5 degree in pitch, roll, and yaw in total. Therefore, none of the participants had to be excluded from the analyses because of head movements. The mean image was co-registered with the whole-brain volume. Imaging data was then normalized into standard stereotaxic MNI space (Montreal Neurological Institute, McGill University, Montreal, Canada). Images were resampled every 2.5 mm using 4th degree spline interpolation to obtain isovoxel and then smoothed with a 8 mm full-width half-maximum (FWHM) Gaussian kernel to accommodate inter-subject variation in brain anatomy and to increase signal-to-noise ratio in the images. The data were high-pass filtered (128s) to remove low-frequency noise components and corrected for autocorrelation assuming an AR(1) process.

The onsets of the four presentation formats (i.e., fractions, decimals, pie charts, dot patterns) were entered as separate conditions in the GLM. As regressors of interest, logarithmic overall distance as first and reaction times as second parametric modulation of the conditions were added on the single-participant level. We decided to use overall distance (instead of reaction times) as the first parametric modulator due to its specific numerical features. Parametric modulators are serially orthogonalised in SPM. Therefore, only variance not explained by the first modulator can be explained by the second modulator. Consequently, logarithmic distance entered the model first, because its inherent numerical quality was of particular interest. Generally, no supra-threshold activation was found for the parametric modulation of RT unless stated otherwise. Movement parameters estimated at the realignment stage of preprocessing were included as covariates of no interest. Brain activation was convolved over all experimental trials with the canonical haemodynamic response function (HRF) as implemented in SPM12 and its time and dispersion derivatives.

We performed a three-stage analysis. First, we evaluated activation associated with the distance effect in all four presentation formats, respectively, to examine specific magnitude-related brain activation in proportion processing. Second, in an exploratory analysis, we examined format-specific activations of both symbolic and non-symbolic relative magnitudes. Third, analogous to previous studies on proportion processing (Jacob & Nieder, 2009a, 2009b), a conjunction analysis was calculated as implemented in SPM12 (conjunction null, see (Nichols, Brett, Andersson, Wager, & Poline, 2005)) to identify brain activation common in all four presentation formats during magnitude processing.

The SPM Anatomy Toolbox (Eickhoff et al., 2005), available for all published cytoarchitectonic maps (www.fz-juelich.de/ime/spm_anatomy_toolbox), was used for anatomical localization of effects where applicable. In areas not yet implemented, the anatomical automatic labelling tool (AAL) in SPM12 (http://www.cyceron.fr/web/aal anatomical_automatic_labeling.html) was used.

If not stated otherwise, thresholds for statistical inference were set at FWE-corrected $p < .05$ at the voxel level, corrected for multiple comparisons at the cluster level to FWE-corrected $p < .05$ with a cluster size of $k = 10$ voxels.

An uncorrected statistical threshold of $p < .001$ was chosen for the conjunction analysis because four conditions of interest needed to significantly modulate the fMRI signal in a given region in the conjunction analysis. The effective *p*-value for a conjunction analysis is the square of the *p*-values for each component. Therefore, a more liberal threshold for such a conservative statistical procedure is justified (Holloway et al., 2010).

6.3 Results

Behavioral results

Mean speed of participants in the four conditions for fractions, decimals, pie charts, and dot patterns, respectively, was: $M_{fractions} = 0.57$ ($SD = 0.15$) items/sec, $M_{decimals} = 1.14$ ($SD = 0.17$) items/sec, $M_{pies} = 0.91$ ($SD = 0.17$) items/sec, and $M_{dots} = 0.60$ ($SD = 0.20$) items/sec. Moreover, mean accuracy in the four conditions for fractions, decimals, pie charts, and dot patterns, respectively, were: $M_{fractions} = 81.1\%$ ($SD = 10.9\%$), $M_{decimals} = 99.2\%$ ($SD = 1.5\%$), $M_{pies} = 91.5\%$ ($SD = 4.8\%$), and $M_{dots} = 72.5\%$ ($SD = 12.6\%$).

In the next step, we ran an LME with condition, distance between proportions as well as their interaction as fixed effects and speed as dependent variable testing for statistical significance of these differences. All three *F*-tests were highly significant [condition: $F(3, 27.97) = 112.77$, $p < .001$, distance: $F(1, 49.81) = 133.76$, $p < .001$, and condition × distance: $F(3, 30.48) = 20.06$, $p < .001$]. This indicated that participants' speed differed between conditions. Pairwise post-hoc comparisons revealed that except for the difference between fractions and dot patterns ($p = .567$) speed in all conditions differed significantly from each other (all $p < .001$). Additionally, the significant distance indicated that across all conditions speed increased with the overall numerical distance, slope = 0.55 items/sec ($SE = 0.05$). However, the significant interaction indicated that distance effects varied between conditions. Mean distance effects (*SE* in parenthesis) in the separate conditions were for fractions: 0.52 (0.07) items/sec, $z = 7.42$, $p < .001$, for decimals: 0.20 (0.05) items/sec, $z = 3.85$, $p < .001$, for pies: 0.77 (0.07) items/sec, $z = 10.39$, $p < .001$, and for dots: 0.69 (0.09) items/sec, $z = 7.40$, $p < .001$, respectively. This indicated that we observed significant distance effects in all four presentation formats. Post-hoc analyses indicated that the distance effect for decimals differed significantly from distance effects of all other presentation formats ($p < .001$). Moreover, distance effects of fractions and pie charts differed significantly from each other (p = .013). Other pairwise comparisons were not significant (p > .139). Figure 6.3A gives an overview of the distance effects for speed data.

We also evaluated performance differences in accuracy between conditions by running a GLME with the same factors. Again, all three LRT for fixed effects were significant [condition: $\chi^2(3) = 210.64$, p < .001, distance: $\chi^2(1) = 100.75$, p < .001, and condition × distance: $\chi^2(3) = 10.28$, p = .016]. Estimated log odds (SE in parenthesis) of the four conditions were for fractions: 1.96 (0.19), in % = 87.6%, for decimals: 6.63 (1.26), in % = 99.9%, for pie charts: 3.641 (0.34), in % = 97.4%, and for dots: 1.30 (0.17), in % = 78.6%, respectively. Pairwise post-hoc comparisons revealed that log odds of all conditions differed from each other significantly (all p < .021). Moreover, the significant distance effect indicated that participants' accuracy increased with the overall numerical distance between two proportions, slope in log odds = 13.69, *SE* = 2.87. However, again the significant interaction between condition and distance indicated that distance effects differed between conditions. Mean distance effects in log odds (*SE* in parenthesis) in the separate conditions were for fractions: 9.37 (1.60), z = 5.86, p < .001, for decimals: 20.57 (10.52), z = 1.96, p = .051, for pie charts: 16.75 (3.02), z = 5.55, p < .001, and for dots: 8.05 (1.25), z = 6.46, p < .001, respectively. Pairwise post-hoc comparisons revealed that only distance effects for dot patterns and pie charts differed significantly (p =.033), whereas all other comparisons were not significant (all p > .067). Distance effects for different conditions are shown in Figure 6.3B.

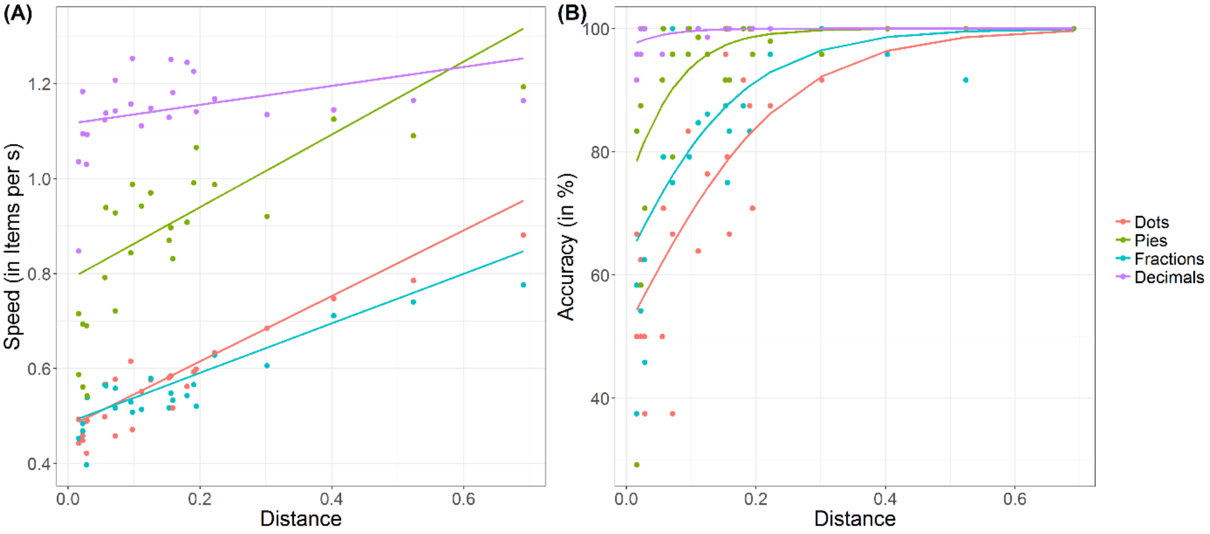


Figure 6.3: Distance effects in the four conditions (dot patterns, pie charts, fractions, and decimals) for (A) speed and (B) accuracy. Accuracy was calculated by transforming log odds into percentages.

Imaging results

Evaluating magnitude processing in different presentation formats

Fractions

Numerical distance in fraction processing was associated with significantly increasing activation in right IPS, bilateral SMA and bilateral frontal gyrus for decreasing distance (see Table 6.1 and Figure 6.4).

Dot patterns

Numerical distance in processing dot patterns was associated with activation in bilateral IPS, left ACC, right SFG as well as visual cortex such as left middle and right inferior occipital gyrus with decreasing distance (see Table 6.1 and Figure 6.4).

Pie charts

Numerical distance in the processing of pie charts revealed activation in bilateral IPS, large bilateral occipital regions extending to parietal and temporal areas and bilateral IFG with decreasing distance. Further activation was observed in bilateral insula, bilateral precentral gyrus and bilateral MCC (Table 6.1 and Figure 6.4).

Decimals

Numerical distance in decimal processing was associated with activation in bilateral IPS, left occipito-temporal regions, left fusiform gyrus and frontal areas with a left-lateralized dominance with decreasing distance. Further clusters of activated voxels were observed in left insula and bilateral precentral gyrus (see Table 6.1 and Figure 6.4).

Table 6.1: Distance effect in proportion magnitude comparison for different presentation formats.

Contrast	Brain region	MNI (x, y, z)			*k*	*t*
fractions	RH Inferior parietal lobule (hIP2)	43	-42	53	31	5.43
	RH Inferior parietal lobule (hIP3)*	46	-45	55		
	RH Supplementary motor area	8	23	45	101	7.59
	LH Supplementary motor area*	-7	18	48		
	LH Middle frontal gyrus	-47	28	33	176	6.58
	LH Inferior frontal gyrus*	-40	21	33		
	LH Middle frontal gyrus	-27	8	50	29	5.92
	RH Precentral gyrus	36	3	30	23	5.73
	LH Superior medial gyrus	-7	33	40	11	5.66

	RH Inferior frontal gyrus	46	31	25	90	6.98
	RH Superior frontal gyrus	21	21	55	34	5.90
dot patterns	RH Superior parietal lobule (hIP3)	33	-52	60	94	6.05
	LH Superior parietal lobule	-30	-57	63	73	6.37
	RH Superior frontal gyrus	26	3	63	41	6.54
	LH Anterior cingulate gyrus	-15	26	28	13	5.97
	RH Calcarine gyrus	12	-70	18	13	5.27
	LH Caudate	-20	6	18	12	5.69
	LH Calcarine gyrus	-17	-75	10	1953	7.75
	LH Middle occipital gyrus*	-42	-80	0		
	LH Cuneus*	-2	-75	18		
	RH Inferior occipital gyrus*	43	-75	-8		
pie charts	RH Middle occipital gyrus	28	-75	33	2094	9.69
	RH Superior occipital gyrus*	26	-75	38		
	RH Inferior occipital gyrus*	43	-75	-5		
	RH Inferior temporal gyrus*	46	-80	-3		
	RH Inferior parietal lobule (hIP2)*	41	-40	48		
	RH Superior parietal lobule (hIP3)*	28	-60	60		
	LH Superior parietal lobule	-22	-65	63	247	6.62
	LH Inferior parietal lobule (hIP3)*	-35	-50	53		
	RH Middle cingulate cortex	8	16	45	836	11.46
	LH Middle cingulate cortex*	-5	18	45		
	RH Precentral gyrus	46	6	28	532	9.32
	RH Inferior frontal gyrus*	48	28	25		
	RH Insula	36	21	3	397	8.93
	RH Inferior frontal gyrus*	33	26	-5		
	LH Insula	-32	18	3	204	9.36
	LH Inferior frontal gyrus	-60	11	25	72	6.41
	LH Precentral gyrus	-45	1	40	37	5.43
	LH Inferior occipital gyrus	-42	-75	-10	1086	11.79
	LH Middle occipital gyrus*	-42	-85	8		
	LH Superior occipital gyrus*	-25	-80	25		
	LH Calcarine gyrus	-15	-72	10	706	8.68
	RH Calcarine gyrus*	16	-67	13		
decimals	RH Inferior parietal lobule (hIP2)	48	-40	45	95	5.96

RH Postcentral gyrus*	43	-32	60		
LH Inferior parietal lobule (hIP3)	-37	-52	58	21	5.41
LH Superior parietal lobule*	-30	-57	63		
LH Inferior parietal lobule	-27	-45	48	12	5.45
LH Supramarginal gyrus	-60	-45	30	24	5.59
LH Lingual gyrus	-15	-55	-10	468	7.38
LH Fusiform gyurs*	-37	-37	-23		
RH Inferior temporal gyrus	51	-62	-10	50	5.83
RH Fusiform gyrus*	41	-57	-13		
LH Inferior occipital gyrus	-45	-75	-13	344	7.60
LH Middle occipital gyrus*	-50	-75	-3		
LH Middle temporal gyrus*	-52	-70	13		
LH Superior temporal gyrus	-42	-35	3	60	7.05
LH Middle temporal gyrus	-55	-55	15	45	5.72
LH Superior temporal gyrus*	-57	-45	15		
RH Temporal pole	51	16	-23	15	5.89
LH Middle temporal gyrus	-57	-37	8	14	5.50
LH Precentral gyrus	-40	-2	40	59	5.81
LH Inferior frontal gyrus	-45	28	-3	47	5.56
LH Inferior frontal gyrus	-42	13	15	29	6.66
RH Superior frontal gyrus	21	-15	75	25	6.21
RH Precentral gyrus	43	-17	58	16	5.32
LH Middle frontal gyrus	-45	26	40	16	5.81
LH Middle frontal gyrus	-35	21	30	12	5.71
LH Posterior Insula	-30	-20	13	28	5.72
LH Insula	-35	21	3	10	5.17
LH Cuneus	-2	-77	18	742	7.51
LH Calcarine gyrus*	-15	-72	13		
LH Superior occipital gyrus*	-12	-80	23		
RH Lingual gyrus	18	-47	-3	43	6.60
LH Putamen	-30	-12	-8	18	5.71
LH Paracentral lobule	-10	-32	75	13	5.11

Activations were thresholded at a whole-brain FWE-corrected *p*-value of < .05 with a cluster size of *k* = 10 voxels and reported only when they remained significant following FWE-correction for multiple comparisons at the cluster-level at *p* < .05 FWE. Cerebellar activations are not reported due to incomplete coverage of the cerebellum depending on individual head size.

Abbreviations: *k* = cluster size; LH = left hemisphere; MNI: Montreal Neurological Institute; RH = right hemisphere; *t* = *t*-value. * Minor maximum.

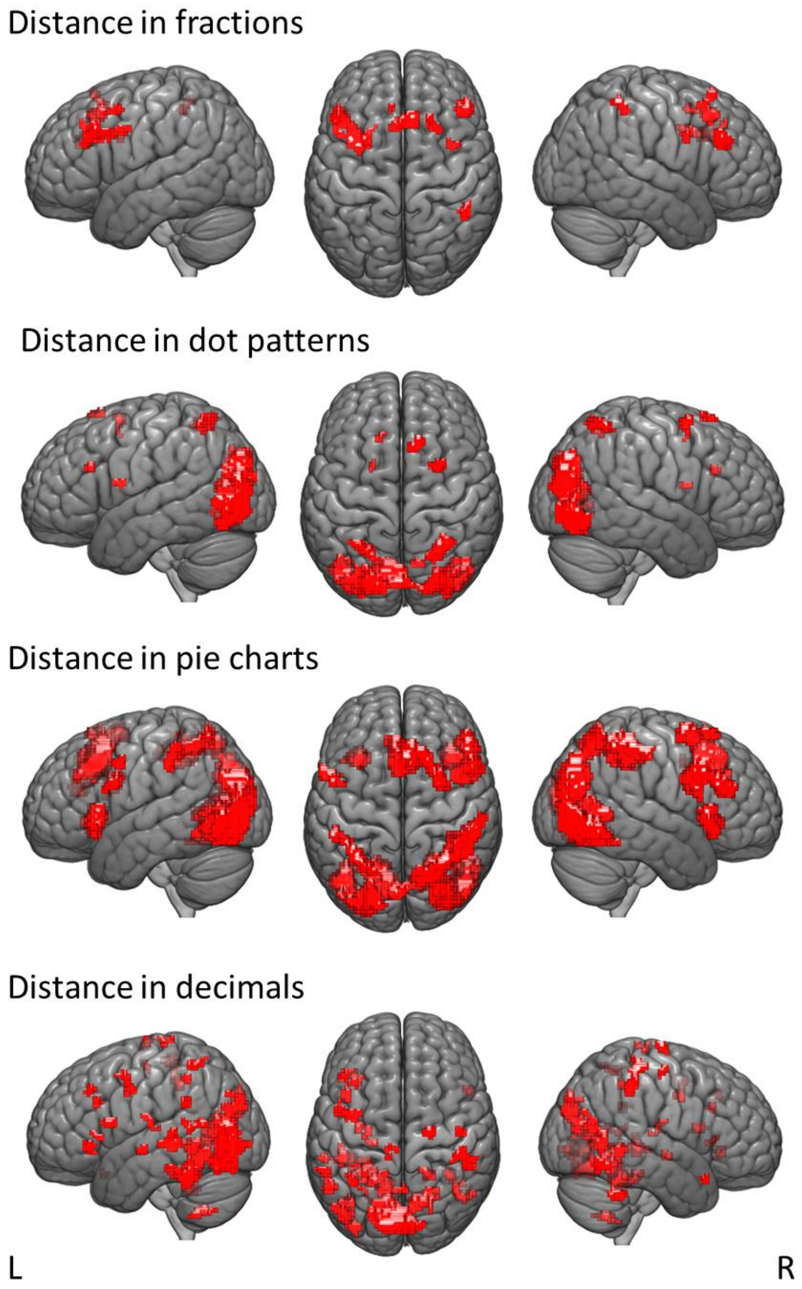


Figure 6.4: Significant patterns of activation found for distance in the four presentation formats fractions, dot patterns, pie charts, and decimals.

Specific correlates of symbolic and non-symbolic proportional magnitudes

Additionally, an exploratory analysis of specific activations associated with processing symbolic and non-symbolic proportional magnitudes was conducted. Because the activation for theses contrasts did not survive FWE-correction on a whole-brain level, activations were thresholded at a whole-brain p-value of < .001 uncorrected and only reported when they remained significant for multiple comparisons at the cluster-level at p < .05 FWE-corrected. This analysis revealed the following results.

Symbolic vs. non-symbolic magnitudes

Distance in processing of symbolic (i.e., fractions and decimals) versus non-symbolic magnitudes (i.e., pie charts and dot patterns) indicated higher activation in bilateral middle frontal gyrus, left SFG, right SMA and left AG (see Table 6.2 and Figure 6.5) with decreasing numerical distance.

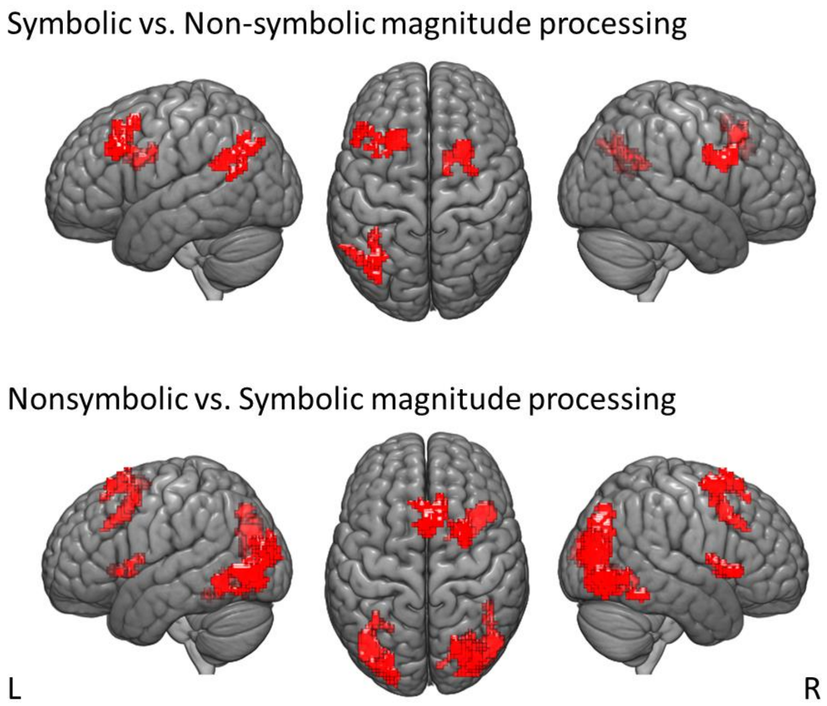
Non-symbolic vs. symbolic magnitudes

Numerical distance in non-symbolic versus symbolic magnitudes was associated with higher activations in a widespread temporal network extending to parietal and occipital cortex, left middle occipital gyrus, right MCC, insula and SFG (see Table 6.2 and Figure 6.5).

Table 6.2: Activations for distance in symbolic vs. non-symbolic as well as non-symbolic vs. symbolic presentation formats.

Contrast	Brain region	MNI (x, y, z)			*k*	*t*
Symbolic vs. non-symbolic	LH Superior frontal gyrus	-20	21	43	286	6.45
	LH Middle frontal gyrus*	-50	23	33		
	LH Angular gyrus	-37	-60	28	273	4.59
	LH Middle occipital gyrus*	-42	-72	33		
	RH Supplementary motor area	21	13	33	229	6.77
	RH Middle frontal gyrus*	26	8	28		
Non-symbolic vs. symbolic	RH Inferior temporal gyrus	48	-72	-5	1046	6.05
	RH Middle occipital gyrus*	33	-75	15		
	RH Superior parietal lobule*	21	-72	43		
	LH Middle occipital gyrus	-40	-75	3	587	5.47
	RH Middle cingulate cortex	8	13	43	390	5.76
	RH Insula	43	23	0	221	4.54
	RH Putamen*	28	3	10		
	RH Caudate Nucleus*	16	13	8		
	RH Superior frontal gyrus	23	6	63	132	5.31

Activations were thresholded at a whole-brain *p*-value of < .001 uncorrected with a cluster size of *k* = 10 voxels and reported only when they remained significant following FWE-correction for multiple comparisons at the cluster-level at *p* < .05 FWE-corrected. Cerebellar activations are not reported due to incomplete coverage of the cerebellum depending on individual head size.
Abbreviations: *k* = cluster size; LH = left hemisphere; MNI: Montreal Neurological Institute; RH = right hemisphere; *t* = *t*-value. * Minor maximum.


Symbolic vs. Non-symbolic magnitude processing

Nonsymbolic vs. Symbolic magnitude processing

Figure 6.5: Activations found for the contrast of distance in symbolic vs. non-symbolic and non-symbolic vs. symbolic presentation formats.

Conjunction analysis of the distance effect

As previous studies evaluated shared neural correlates of magnitude processing for fractions and fraction words, we conducted a conjunction analysis ((Ischebeck et al., 2009; Jacob & Nieder, 2009a); conjunction null, see (Nichols et al., 2005)) to evaluate the hypothesis of a common neural correlate of magnitude processing for symbolic and non-symbolic proportions. The conjunction analysis revealed significant joint activation in right SPL (hIP3) as well as bilateral occipital regions (see Table 6.3 and Figure 6.6).

Table 6.3: Joint activations across the four conditions (i.e., fractions, decimals, dot patterns, pie charts) for distance as revealed by the conjunction analysis.

Contrast	Brain region	MNI (x, y, z)			*k*	*t*
Conjunction	RH Superior parietal lobule (hIP3)	31	-60	60	46	4.50
	LH Calcarine gyrus	-17	-75	13	276	5.55
	RH Calcarine gyrus*	16	-67	18		
	LH Cuneus*	-2	-75	20		

RH Superior occipital gyrus*	23	-75	28		
LH Inferior occipital gyrus	-40	-72	-8	76	4.76
LH Superior occipital gyrus	-25	-70	30	73	4.60
RH Middle occipital gyrus	46	-82	0	22	3.88
RH Inferior occipital gyrus*	43	-80	-3		

Activations were thresholded at a whole-brain *p*-value of < .001 uncorrected with a cluster size of *k* = 10 voxels. Cerebellar activations are not reported due to incomplete coverage of the cerebellum depending on individual head size. Abbreviations: *k* = cluster size; LH = left hemisphere; MNI: Montreal Neurological Institute; RH = right hemisphere; *t* = *t*-value. * Minor maximum.

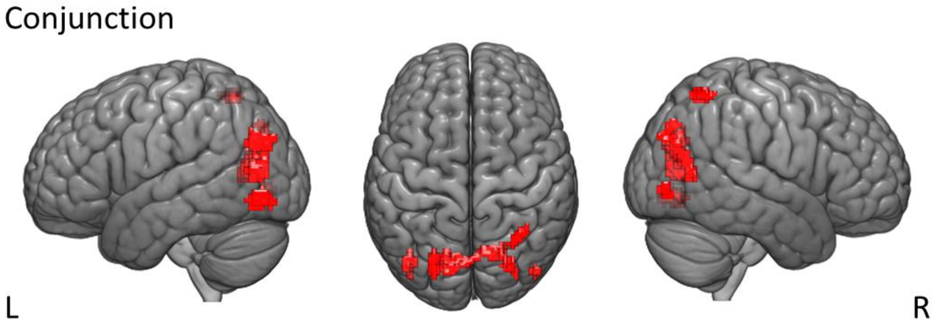


Figure 6.6: Significant joint activation across the four conditions for distance (e.g., fractions, decimals, dot patterns, pie charts).

6.4 Discussion

The present study aimed at investigating whether the processing of symbolic and non-symbolic proportions draws on a common underlying neural substrate. Recent neuroimaging evidence indicated that symbolic fractions (Ischebeck et al., 2009; Jacob & Nieder, 2009a) and non-symbolic proportions (Jacob & Nieder, 2009b) are processed within a fronto-parietal network including the IPS. Synced with evidence on whole number processing (e.g., Arsalidou & Taylor, 2011; Dehaene et al., 2003 for overviews) this suggests that both absolute and relative magnitude information seem to be processed within this brain area. Nevertheless, a systematic evaluation of brain areas jointly activated when processing symbolic *and* non-symbolic proportion magnitude was missing so far. Therefore, we systematically evaluated the neural correlates of processing symbolic fractions and decimals as well as non-symbolic dot patterns and pie charts in the same experiment. Most importantly, we observed evidence for a common neural substrate in right IPS as well as bilateral visual cortex for processing relative magnitude irrespective of presentation format. In the following, we will first discuss this joint activation found for symbolic and non-symbolic proportions before addressing distance-related activation observed for symbolic and non-symbolic formats and in each presentation format separately.

A common neural substrate for processing relative magnitude

We observed a common neural substrate for processing symbolic and non-symbolic proportions in an occipito-parietal network comprising the right IPS. Within this network, IPS activation seems to reflect processing of abstract relative magnitude (e.g., Eger et al., 2003; Pinel et al., 2001, 2004; Venkatraman et al., 2005), whereas activation in occipital areas might rather reflect higher order visual processing as well as decoding of the visual form (Ansari, 2008; Fias et al., 2013; Jolles et al., 2016), which helps to process semantic features of quantity.

Recent research revealed a right-hemispheric preference for the processing of absolute number magnitude (Chochon et al., 1999; Dehaene, 1996; Pinel et al., 2001). As such, the right IPS seems to specifically underlie the semantic representation of numerical distances (Mussolin, Noel, Pesenti, Grandin, & De Volder, 2013). This right-hemispheric preference for the processing of magnitude was reported for both symbolic and non-symbolic quantities (e.g., Piazza et al., 2007). Importantly, our data showed joint activation for magnitude processing of symbolic and non-symbolic proportions in an occipito-parietal network including the right IPS. Thus, besides absolute magnitude also relative magnitude information seems to be processed in right IPS, irrespective of presentation format. Importantly, this seems to reflect a neural correlate of an abstract concept for relative magnitude. This is in line with propositions of the triple code model of numerical cognition that numerical magnitude and mental arithmetic are represented and processed within the IPS (Arsalidou & Taylor, 2011; Dehaene & Cohen, 1995, 1997; Dehaene et al., 2003). Importantly, recent evidence suggested that the respective parietal cortex areas might subserve an abstract, notation-independent representation for both absolute and relative magnitude (DeWolf, Chiang, Bassok, Holyoak, & Monti, 2016; Ischebeck et al., 2009; Jacob & Nieder, 2009b, 2009a; Pinel et al., 2001, but see Kadosh & Walsh, 2009 for a more detailed discussion of this point). The results of our conjunction analysis support this assumption. Moreover, our data also extended previous research on proportion processing because so far only the processing of either symbolic fractions (Ischebeck et al., 2009), fractions and fraction words (Jacob & Nieder, 2009a) or non-symbolic proportions (Jacob & Nieder, 2009b) was investigated on the neural level. In the present study, we systematically investigated common neural activation for the processing of both symbolic and non-symbolic formats. Our results are also in line with recent research suggesting that humans (and animals) are not necessarily born with a “sense of number” – the ability to perceive, manipulate and understand discrete numerosities (Cantlon, Platt, & Brannon, 2009;

Dehaene, 1997; Feigenson, Dehaene, & Spelke, 2004) – but rather a generalized and abstract "sense of magnitude" for the processing of both, numerosities and continuous magnitudes (e.g., size, area, and density; for a review, see Leibovich, Katzin, Harel, & Henik, 2017). As the present study found a shared neural correlate for both discrete (e.g., fractions and dot patterns) as well as continuous relative magnitudes (e.g., decimals and pie charts) in symbolic and non-symbolic presentation formats, the results further support the idea of such a generalized magnitude system.

Additionally, we found activation in bilateral visual cortex (bilateral superior, bilateral inferior, right middle occipital gyrus). These brain regions are involved in higher order visual processing and decoding of the visual form (Ansari, 2008; Fias et al., 2013; Jolles et al., 2016). Furthermore, the ventral visual stream is anchored in the lateral occipital cortex (LOC; Menon, 2015). This stream plays an important role in number representation and magnitude manipulation as it interacts with the IPS for the semantic representation and procedural manipulation of quantity (Menon, 2015). Importantly, the ventral visual stream areas in the occipital gyrus are not only co-activated with the IPS during numerical and arithmetic processing, but their activation also increases with task complexity (Keller & Menon, 2009; Menon, 2015; Rosenberg-Lee, Tsang, & Menon, 2009). Hence, our data point to higher order visual processing during relative magnitude processing in the ventral visual stream which may reflect the complexity of accessing relative magnitude information.

This task complexity might also be reflected by the distance effect, an effect that is often associated with task difficulty as difficulty increases when the distance between two to-be-compared numbers decreases (Moyer & Landauer, 1967). The distance effect for symbolic and non-symbolic proportions was observed in the behavioral data. We found differences in distance effects for error rates and reaction times between the different presentation formats. While error rates and reaction times were highest for fractions and dot patterns, comparing pie charts – and even more so decimals – led to faster and more accurate responses. Increasing response times and error rates might reflect influences of task difficulty. Therefore, behavioral data seemed to indicate that accessing magnitude information of proportional relations might not be the only mechanisms involved. This is also reflected in the neural data.

The IPS was previously associated with tasks requiring specific attention due to higher levels of difficulty (Culham et al., 1998; Culham & Kanwisher, 2001; Shuman & Kanwisher, 2004). In studies on number processing the distance effect is a prominent paradigm (e.g., Ischebeck et al., 2009; Pinel et al., 2001). However, this effect is strongly modulated by difficulty: as the distance between two numerals decreases, error rates as well as response times, and hence, difficulty increases. Thus, the observed activation in IPS during numerical tasks might also be driven by task difficulty. Yet, previous studies found activations in the IPS for either passive listening to number words (Klein, Moeller, Nuerk, & Willmes, 2010) or passive viewing of symbolic numbers versus letters and colors (Eger et al., 2003). Therefore, we are confident that particularly activation in right intraparietal regions, as observed in the present conjunction analysis, reflects processing of (relative) magnitude information over and beyond influences of task difficulty.

Specific activations for symbolic and non-symbolic presentation formats

The contrast between symbolic (i.e., fractions and decimals) and non-symbolic presentation formats (i.e., dot patterns and pie charts) indicated activation in a fronto-parietal network comprising left AG, left superior and middle frontal gyrus, and right SMA. In line with previous research, activation found for symbolic vs. non-symbolic proportions showed a left-lateralized preference (Venkatraman et al., 2005).

The left AG has been previously associated with verbally-mediated processes such as the retrieval of arithmetic facts and symbolic numerical processing (Dehaene et al., 2003, 1999; Grabner et al., 2009; Holloway et al., 2010). Holloway and colleagues (Holloway et al., 2010) argued that the left AG mediates the mapping between a visual form and its semantic referent, that is, between numerical symbols and their magnitudes. However, recent research indicated that the AG plays a more domain-general attentional role that may not be specific to math fact retrieval (Bloechle et al., 2016; Rosenberg-Lee, Chang, Young, Wu, & Menon, 2011). In particular, Bloechle and colleagues (Bloechle et al., 2016) proposed that the left AG adjusts and adapts relative attentional demands in the neural networks associated with fact retrieval and magnitude manipulation. For accessing magnitude information of decimals a symbol-to-referent mapping in the left AG seems plausible. However, accessing the magnitude of a fraction might require additional computational steps. This might involve increased attentional effort or more demanding symbol-to-referent mapping during the decoding of several numerals of the fraction itself. Thus, the role of the left AG in our data might reflect both scenarios – higher attentional demands or symbol-to-referent mapping.

Furthermore, activation of the left SFG and right SMA may be assumed to reflect goal creation, procedural steps as well as the generation of strategies for solving multi-step problems during the processing of symbolic proportions (Arsalidou & Taylor, 2011).

In contrast, processing non-symbolic proportions indicated specific activation within the ventral visual stream (bilateral middle occipital gyrus, right inferior temporal gyrus, and right superior parietal lobule), right insula, left MCC, and right SFG. The large cluster of bilateral occipital activation might reflect higher visual demands of the non-symbolic presentation formats. Furthermore, activation of the ventral visual stream might point to the involvement of visuo-spatial functions and covert shifts of attention during processing non-symbolic proportions (Menon, 2015). In particular, the superior parietal lobe was repeatedly reported for non-symbolic number processing (Ansari et al., 2006; Holloway et al., 2010; Piazza et al., 2004, 2007) and suggested to host a visual-spatial representation of quantity (Ansari, 2008).

Moreover, higher activation of areas associated with cognitive control comprising, amongst others, MCC and SFG might indicate that accessing magnitude information of non-symbolic proportions required stronger involvement of cognitive control processes and performance monitoring than of symbolic proportions (MacDonald, Cohen, Stenger, & Carter, 2000). Furthermore, we suggest that the involvement of the SFG might reflect the application of strategies for solving multi-step problems (Arsalidou & Taylor, 2011). Together with higher activation of areas subserving cognitive control, the right insula was suggested to be involved in initiating motivated behavior (Uddin & Menon, 2009), execution of responses (Huettel, Guzeldere, & McCarthy, 2001), and error processing (Hester, Fassbender, & Garavan, 2004; see also Arsalidou & Taylor, 2011).

Distance-related activation = magnitude-related representation?

We also evaluated magnitude-related activation in proportion processing by specifically focusing on the neural correlates of distance in the respective presentation formats. Our findings indicated that processing relative magnitude of symbolic and non-symbolic proportions might not exclusively reflect domain-specific magnitude-related processing. Rather, our results suggest that the idea of a unique reflection of (relative) magnitude processing by distance may be too simplistic. In fact, magnitude processing of proportions might not only reflect specific processing of magnitude information, but may also reflect influences of other less domain-specific cognitive processes involved in distance-related processing. In particular, it seems that different presentation formats contain different cognitive components to different degrees. In the following, we will discuss these differing components as indicated by observed activation of associated brain areas in the current study.

Activation in (intra)parietal cortex

Bilateral IPS was repeatedly reported active for processing absolute magnitude (Dehaene et al., 2003; Eger et al., 2003; Pinel et al., 2001, 2004). In line with this idea, we found that magnitude processing of *decimals* was associated with activation in the bilateral IPS, most probably reflecting the processing of number magnitude information (DeWolf et al., 2016; Mussolin et al., 2013; Piazza et al., 2007). In fact, magnitude processing of decimals is very similar to processing absolute magnitude because skipping the leading 0 and just comparing the digits following the decimal point leads to a correct result (DeWolf et al., 2016). Thus, no computation of part-whole relations, and thus, relative magnitude is necessary to access magnitude information of decimals compared to the other presentation formats used in this study. Consequently, the involvement of intraparietal regions typically involved in processing absolute magnitude comes as no surprise.

In line with previous research, our data also revealed activation in right IPS for the magnitude processing of *fractions* (Ischebeck et al., 2009). Because the right IPS was repeatedly reported to be activated during absolute number magnitude processing in number comparison tasks (Chochon et al., 1999; Dehaene, 1996; Mussolin et al., 2013; Piazza et al., 2007), our data on the processing of relative magnitude extend these previous findings. In particular, our results indicate that in addition to absolute numerical magnitude, relative magnitude of symbolic proportions is also processed in the IPS. This is significant because additional computational steps may be necessary to access magnitude information of proportions. These findings, thus, further support previous results suggesting that the right IPS is systematically involved in the processing of number magnitude, regardless of number format (Piazza et al., 2007) or notation (Pinel et al., 2001).

For the magnitude processing of *dot patterns* we found activation in the bilateral SPL extending to the IPS in the right hemisphere, which has been repeatedly reported for non-symbolic number processing (Ansari et al., 2006; Holloway et al., 2010; Piazza et al., 2004, 2007). While activation of the right IPS might indicate additional computations of part-whole relations necessary for accessing relative magnitude information, activation of bilateral SPL rather reflects the involvement of visuospatial functions such as saccades and covert shifts of attention (Menon, 2015). This finding seems plausible for this presentation format because eye-movements and attention shifts are particularly necessary to capture discrete quantities and the part-whole relation reflected by proportional dot patterns.

Moreover, we found activation in bilateral IPS and SPL for the magnitude processing in *pie charts*. It has been shown that bilateral IPS is activated during estimation strategies and approximation processes for symbolic and non-symbolic presentation formats (Castelli, Glaser, & Butterworth, 2006; Piazza, Mechelli, Price, & Butterworth, 2006; Venkatraman et al., 2005). To a certain degree, activation in bilateral superior and inferior parietal lobes might also indicate the involvement of mental rotation strategies (Alivisatos & Petrides, 1997; Jordan, Heinze, Lutz, Kanowski, & Jäncke, 2001). Thus, parietal activation might reflect an additional distance effect caused by the angular degrees between the to-be-compared blue parts of the pie charts. However, as we found joint activation for all presentation formats in right IPS (with the other three formats not requiring mental rotation), parietal activation in magnitude processing of pie charts should reflect not only mental rotation strategies, but at least partially the processing of relative magnitude information as well. This might indicate the involvement of estimation, approximation and mental rotation strategies during accessing relative magnitude information for this specific presentation format.

Activation in frontal cortex areas

Furthermore, we observed activation in bilateral inferior and middle frontal gyrus as well as SMA for the magnitude processing of *fractions*. Activation in frontal areas is commonly associated with rather domain-general supplementary executive processes such as strategy choice and procedural planning in numerical cognition (Dehaene & Cohen, 1995; Grabner et al., 2009; Klein et al., 2016). Furthermore, increasing demands on working memory, performance monitoring, goal-directed problem solving, and interference control loads were associated with neural activation in a network comprising these frontal brain regions including IFG, ACC, MCC, and insula (Fias et al., 2013; Lui, Banich, Jacobson, & Tanabe, 2004; Peterson et al., 2002). Importantly, the insular-cingulate salience network which initiates control signals during arithmetic problem solving is anchored in the anterior insula and ACC (Menon, 2015; Supekar & Menon, 2012). In line with this rationale, participants may have applied different strategies which involve executive processes for accessing relative magnitude information of fractions. Observed activation in frontal areas might reflect increasing demands on such executive processes during magnitude computation of fractions, and thus, might reflect the active magnitude computation of the given part-whole relation. These computations can be very demanding, and thus, lead to high loads on executive functions. Hence, activation of frontal areas might reflect aspects of difficulty in actually computing relative fraction magnitude and, consequently, additional computational strategies necessary for doing so.

Importantly, it was shown that context-dependent shifts in strategy might also cause differences in activation of frontal brain regions (Wagner, Desmond, Glover, & Gabrieli, 1998). Thus, frontal areas might be activated differently according to which strategy is applied for accessing relative magnitude information for the respective proportion and how high the demand on executive functions actually is. This is also reflected by the results of our conjunction analysis as we did not find joint frontal activation for all presentation formats. However, each presentation format elicited seperate activation in specific frontal brain regions. Yet, these brain regions apparently did not overlap. Hence, different strategies seemed to be applied for accessing magnitude information of the respective presentation formats which, in turn, may have led to distinct activations in frontal areas.

Magnitude processing of *decimals* elicited activation in IFG, MFG and insula exclusively in the left hemisphere. IFG is typically involved in processing simple numerical tasks with low working memory or procedural requirements, while MFG and insula rather tend to support working memory systems and goal-directed attention maintenance (Arsalidou & Taylor, 2011; Fias et al., 2013; Majerus et al., 2010).

For *pie charts*, computations of part-whole relations and visual strategies might play a crucial role for accessing relative magnitude information. Again, applying these visual estimation strategies and computations might have led to increased working memory demands as reflected by activation of bilateral IFG (Bunge, Kahn, Wallis, Miller, & Wagner, 2003; Taillan et al., 2015). Thus, activation in bilateral IFG, bilateral MCC as well as bilateral insula observed for magnitude processing of *pie charts* may indicate the involvement of the salience network as well as working memory and goal-directed attention processes also in this presentation format (Menon, 2015; Supekar & Menon, 2012).

We observed activation in left ACC and the right SFG for the magnitude processing of *dot patterns*. These activations indicated specific demands on working memory and cognitive control when accessing magnitude information of proportional dot patterns (Arsalidou & Taylor, 2011; Ischebeck et al., 2009). In particular, the involvement of the SFG may further reflect the generation of strategies for solving multi-step problems (Arsalidou & Taylor, 2011). Hence, to access magnitude information of proportional dot patterns, participants seem to apply multi-step strategies for summation and quantification of non-symbolic part-whole relations, which in turn lead to increased working memory and cognitive control demands.

Activation of occipital brain areas

Previous studies showed that high attentional loads in visual processing, encoding, and reanalysis, as well as visual manipulations evoke activations in occipital areas (Pinel et al., 2004; Somers, Dale, Seiffert, & Tootell, 2006; Wood, Nuerk, & Willmes, 2006). We found activation in these brain regions for magnitude processing of both *pie charts* as well as *dot patterns*. Thus, accessing magnitude information of pie charts seems to recruit a wide range of executive processes and visual strategies, which are associated with a wide range of brain activations in fronto-parietal and occipital regions.

Magnitude processing of *dot patterns* was associated with activation of occipital brain regions involved in processing visual information. This activation in bilateral occipital gyri, thus, might reflect the specific processing demands on visual information to access magnitude information in this presentation format. Activation in visual cortex might be even stronger when participants drive their attention to a specific object, i.e. proportional dot patterns or pie charts (Müller & Kleinschmidt, 2003). Thus, to derive relative magnitude information of dot patterns and pie charts participants seemed to strongly rely on visual strategies. In particular, accessing magnitude information for non-symbolic proportions might be associated with increasing visual processing demands, and thus, with increasing activation in visual areas.

Furthermore, we also found activation in the left occipital gyrus extending to fusiform gyrus, occipitotemporal areas as well as middle and superior temporal gyrus associated with magnitude processing of *decimals*. Interestingly, the ventral visual stream areas consisting, amongst others, of lateral occipital cortex, fusiform gyrus and inferior temporal cortex were co-activated with the IPS during arithmetic processing (Menon, 2015). In this context, activation in occipitotemporal regions including the fusiform gyrus might indicate the involvement of the visual number form area during magnitude processing (Dehaene & Cohen, 1995). Although speculative, an explanation for this finding might be that participants had to visually encode more digits in trials with smaller distance. The smaller the distance, the further to the right in the digit string the decisive digit is to be found (e.g., 0.24_0.75 vs. 0.53_0.56). Thus, more digits had to be encoded visually to access the respective magnitude information. Visually encoding digits might in turn have led to increased activation in the visual number form area and the occipital gyrus. Additionally, activation in left superior temporal regions, which are typically involved in reading processes (Raij, Uutela, & Hari, 2000; Van Atteveldt, Formisano, Goebel, & Blomert, 2004), may reflect the connection between numerical symbols and their quantitative referents (Holloway et al., 2010). Interestingly, however, we failed to find activation in the visual number form area associated with the magnitude processing of fractions. This might indicate that the difficulty of this specific presentation format and cognitive demands during the additional computational steps for accessing magnitude information of fractions might be predominant over visual encoding processes. Furthermore, although previous studies suggested that fractions are represented holistically in the human brain (Ischebeck et al., 2009), our results suggest that access to the magnitude information of a fraction seems to involve additional computational steps as reflected by activation of frontal working memory and cognitive control areas rather than a simple symbol-to-referent mapping. This might also explain why we did not observe any activation in the visual number form area for magnitude processing of fractions.

Practical implications of our study

From a more practical perspective, the neurocognitive results presented here might indicate that a shared use of symbolic and non-symbolic presentation formats could be supportive for teaching and learning fractions because they activate a joint neural correlate reflecting abstract relative magnitude processing. Moreover, it is known that learning with multiple representations can enhance students' understanding of new concepts (Ainsworth, 2006). However, teaching fractions currently focuses strongly on memorization of procedures and not on conceptual understanding (Lortie-Forgues, Tian, & Siegler, 2015; Obersteiner, Dresler, Bieck, & Moeller, 2018). Yet, in order to choose the appropriate procedure to solve fraction problems, these procedures should be underpinned by good conceptual knowledge about fractions (Swan, 2001). An intervention study of Gabriel and colleagues (Gabriel et al., 2012) showed that the use of non-symbolic presentation formats to represent and manipulate fractions improved students' conceptual understanding of fractions and their magnitudes. Additionally, an intelligent tutoring system as described by Rau and colleagues (Rau et al., 2012) enhanced the conceptual understanding of fraction magnitude by specifically associating symbolic fractions with non-symbolic presentation formats. After working with this tutoring system as part of their regular mathematics instructions, 4th- and 5th-grade students improved significantly in their conceptual understanding of fractions (for an overview, see Obersteiner et al., 2018).

Although speculative, these positive effects when jointly using symbolic and non-symbolic presentation formats for teaching conceptual understanding of fractions, might be partly based on a shared neural correlate for relative magnitude processing. However, the benefit of jointly using symbolic and non-symbolic formats might be additionally driven by complementary mechanisms in relative magnitude processing of different presentation formats: in addition to the shared neural correlate, all presentation formats showed distinct and specific activation patterns in the current study, which points to different additional (sub)processes that are linked to each presentation format. Because these (sub)processes differ for all presentation formats, non-symbolic presentation formats might complement symbolic formats and vice versa for conceptual understanding. Thereby, children who do not excel at understanding a particular presentation format might be able to compensate for these difficulties by means of other formats. The processing pathways for the presentation formats seem to differ partially depending on the format but to finally converge to abstract magnitude processing in the right IPS.

Thus, the present findings seem to support previous findings of intervention studies on the conceptual understanding of fractions and proportions from a neurocognitive perspective and vice versa.

Conclusion

Regions around the IPS are commonly associated with the processing of absolute magnitude (e.g., Piazza et al., 2007; Pinel et al., 2001). However, recent research indicated that also relative magnitude information is associated with activation in parietal brain regions (DeWolf et al., 2016; Ischebeck et al., 2009; Jacob & Nieder, 2009a, 2009b). Thus, brain areas involved in processing absolute magnitude of numbers were also activated during processing relative magnitude of symbolic fractions as well as non-symbolic proportions. Here, we investigated systematically whether the processing of symbolic and non-symbolic proportions draws on shared underlying neural correlates. Results of the present study indicated joint activation of specific occipito-parietal areas, including right IPS for both symbolic and non-symbolic proportions. In particular, the right IPS is associated with number magnitude processing (Dehaene, 1996; Mussolin et al., 2013; Piazza et al., 2007; Pinel et al., 2001), while the occipital activation during magnitude processing rather reflects the higher order visual processing, which contributes to building semantic representations of quantity (Ansari, 2008; Fias et al., 2013; Jolles et al., 2016). Thus, our findings indicate a shared neural substrate for a format-independent, abstract concept of relative magnitude.

Yet, our results may also be influenced by task difficulty. Nevertheless, activations in the IPS cannot be attributed to task difficulty exclusively, but also reflected specific processing of relative magnitude information. Furthermore, influences of task difficulty might rather be reflected by observed activation in frontal areas due to increasing demands on executive functions. Interestingly, we did not observe joint frontal activation for all presentation formats although all presentation formats elicited significant activation in frontal brain regions. This might indicate that participants applied different strategies depending on the respective presentation format. For instance, while demands on cognitive control and working memory may be lower for magnitude processing of decimals, magnitude processing of fractions might rather be associated with additional computational steps, and thus, with higher demands on working memory and cognitive control. Furthermore, participants might use estimation strategies for magnitude processing of pie charts whereas summation and quantification strategies might support magnitude processing of dot patterns.

Nevertheless, the present data provide evidence for a shared neural correlate for processing relative magnitude, irrespective of symbolic or non-symbolic presentation format.

Declarations

Ethics approval and consent to participate

The study was approved by the local ethics committee of the medical faculty of the University of Tuebingen. Written informed consent was obtained from all participants.

Consent for publication

Not applicable.

Availability of data and materials

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Competing interests

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Authors' contributions

KM and EK conceived the study. KM, EK, and SH participated in its design. JB, JB, and JR performed data collection. JM, SH, and JFD performed processing and statistical analyses. JM and SH drafted the manuscript; all other authors revised it critically. All authors contributed to the interpretation of the data. All authors read and approved the final manuscript.

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7 Study 2: Processing symbolic and non-symbolic proportions - Domain-specific numerical and domain-general processes in intraparietal cortex[9]

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Abstract

Previous studies on the processing of fractions and proportions focused mainly on the processing of their overall magnitude information in the intraparietal sulcus (IPS). However, the IPS is also associated with domain-general cognitive functions beyond processing overall magnitude, which may nevertheless be involved in operating on magnitude information of proportions. To pursue this issue, the present study aimed at investigating whether there is a shared neural correlate for proportion processing in the intraparietal cortex *beyond* overall magnitude processing and how part-whole relations are processed on the neural level. Across four presentation formats (i.e., fractions, decimals, dot patterns, and pie charts) we observed a shared neural substrate in bilateral inferior parietal cortex, slightly anterior and inferior to IPS areas recently found for overall magnitude proportion processing. Nevertheless, when evaluating the neural correlates of part-whole processing (i.e., contrasting fractions, dot patterns, and pie charts vs. decimals), we found wide-spread activation in fronto-parietal brain areas. These results indicate involvement of domain-general cognitive processes in part-whole processing beyond processing the overall magnitude of proportions. The dissociation between proportions involving part-whole relations and decimals was further substantiated by a representational similarity analysis, which revealed common neural processing for fractions, pie charts, and dot patterns, possibly representing their bipartite part-whole structure. In contrast, decimals seemed to be processed differently on the neural level, possibly reflecting missing processes of actual proportion calculation in decimals.

7.1 Introduction

Recent research indicated that processing natural numbers and proportions is associated with activation in the intraparietal sulcus (IPS; Piazza, Pinel, Le Bihan, & Dehaene, 2007; Sokolowski, Fias, Mousa, & Ansari, 2017; see Nieder, 2005 for a review). Furthermore, we recently showed that processing overall magnitude of symbolic and non-symbolic proportions draws on similar neural correlates in the IPS (Mock et al., 2018). However, the IPS is not specifically dedicated to number processing. As part of the higher order (also referred to as tertiary) association cortex, the IPS hosts a variety of fine-grained sensory, motor, and cognitive functions including attention orienting, grasping, spatial working memory, saccade planning, mental rotation, and navigation (Culham and Kanwisher, 2001; Humphreys and Lambon Ralph, 2017, 2015; Simon et al., 2002).

However, joint aspects of processing proportions beyond overall magnitude have not yet been systematically investigated at the neural level. By the term *beyond overall magnitude* we refer to domain-specific numerical and domain-general processes involved in proportion processing as compared to the specific processing of overall proportion magnitude as reflected by the distance effect (Mock et al., 2018) and, thus, to processes not necessarily limited to magnitude processing. As such, the aim of the present study was to investigate shared aspects of processing proportions in the IPS reflecting domain-specific numerical as well as domain-general processes. In other words, we suggest that the neural activations evaluated in the present study do not necessarily reflect overall magnitude processing as indicated by the numerical distance effect (Mock et al., 2018). Nevertheless, processing magnitude information might still play an important role in proportion processing when operating on the actual proportion. This might, however, rather involve more top-down regulated proportion processing including domain-specific magnitude-related processes *and* other domain-general cognitive mechanisms.

Processing proportions seems particularly suited for this purpose as their processing is more difficult and requires more steps than just accessing number magnitude information. Furthermore, we evaluated whether different presentation formats (i.e., symbolic and non-symbolic presentation formats) of the same concept (i.e., proportions) share underlying domain-specific numerical as well as domain-general neural processes.

In the following, we will first present recent neuroimaging evidence on the processing of symbolic fractions and non-symbolic proportions. However, because neuroimaging studies in numerical cognition have so far focused mainly on the IPS as the core area for number magnitude processing, we then also introduce the role of the intraparietal cortex for more domain-general cognitive processes that are not necessarily specific to processing proportion magnitude, such as visuo-spatial processing, attention orienting, mental rotation, saccades, or spatial working memory.

The neural underpinnings of (proportion) number processing

Previous studies showed that a bilateral fronto-parietal network centered around the IPS is associated with number processing (Piazza, Pinel, Le Bihan, & Dehaene, 2007; see Nieder, 2005 for a review). Within this network, the IPS seems to be specifically involved in the processing of numerical magnitude information (Piazza et al., 2007; Pinel et al., 2001) and mental calculation (Arsalidou and Taylor, 2011; Dehaene et al., 1999). Furthermore, it was observed that bilateral inferior parietal lobule (IPL) and precuneus, left superior parietal lobule (SPL) and right superior frontal gyrus (SFG) are involved in processing of both symbolic and non-symbolic numbers (Sokolowski et al., 2017). More specifically, left intraparietal cortex as well as the left angular gyrus and right supramarginal gyrus seem to be involved in the processing of symbolic numbers, exact calculation, and arithmetic fact retrieval (Dehaene et al., 1999; Grabner et al., 2009; Holloway et al., 2010; Simon et al., 2002; Sokolowski et al., 2017; Venkatraman et al., 2005). In contrast, the right IPS seems to underlie a semantic representation of numbers and an abstract code for absolute and relative magnitude (Cohen Kadosh et al., 2007; Mock et al., 2018; Mussolin et al., 2013). Additionally, a right-lateralized fronto-parietal network including right SPL and IPL, right SFG and right middle occipital gyrus seem to be specifically activated in the processing of non-symbolic numerosities (Holloway et al., 2010; Sokolowski et al., 2017). This suggests that symbolic and non-symbolic numbers are processed using both overlapping and distinct neural substrates (Sokolowski et al., 2017).

Furthermore, recent studies also revealed that brain regions typically associated with natural number processing are also involved in processing proportions (Ischebeck et al., 2010, 2009a, Jacob and Nieder, 2009a, 2009b). For instance, Jacob and Nieder (2009a) observed that the processing of symbolic fraction magnitude within the bilateral IPS seems to be independent of the presentation format and suggested that the same populations of neurons code the same fraction magnitude. Importantly, Jacob and Nieder (2009b) observed similar intraparietal effects for non-symbolic proportions. This is substantiated by a recent study, in which we found that processing symbolic (i.e., fractions and decimals) and non-symbolic proportions (i.e., dot patterns and pie charts) share a neural correlate in occipito-parietal regions including the right IPS (Mock et al., 2018). Interestingly, in our study (Mock et al., 2018), joint IPS activation was observed to be specific for the processing of overall symbolic and non-symbolic proportion magnitude (see also Ischebeck et al., 2009a; DeWolf et al., 2016).

Thus, on the neural level proportion magnitude seems to be represented by its value as a whole (i.e., its relative magnitude; Ischebeck et al., 2009a; Jacob & Nieder, 2009b). Based on this notion, DeWolf and colleagues (2016) investigated whether different symbolic numbers (i.e., fractions, integers, decimals) map onto a joint abstract magnitude code or whether different representations exist for specific number types (integers versus symbolic proportions) or number notations (fractions vs. base-10[10], e.g. ½ vs 0.5). Interestingly, processing fractions, integers, and decimals activated areas in the IPS. However, fractions yielded a distinct activation pattern from decimals and integers within the IPS, as revealed by both univariate and multivariate analyses. Thus, neural processing seemed to be sensitive to number notation (fractions vs. base-10), but not to number type (integer vs. proportion).

Taken together, previous work indicated that similar intraparietal brain regions are involved in number magnitude processing of integers as well as the magnitude processing of proportions, irrespective of symbolic or non-symbolic presentation format (for a brief overview on the processing of symbolic and non-symbolic proportions, see Jacob, Vallentin, & Nieder, 2012).

Yet, previous studies on the processing of proportions mainly focused on the processing of their magnitude in the IPS. However, recent research showed that the intraparietal cortex hosts other (related), more domain-general functions (e.g., Knops, Thirion, Hubbard, Michel, & Dehaene, 2009; Simon et al., 2002). This is in line with arguments from an evolutionary point of view that number processing co-opts brain regions that support these related functions rather than relying on a specifically dedicated brain region (Dehaene and Cohen, 2007; Knops et al., 2009). In the following, number unspecific processes subserved by the intraparietal cortex will be briefly summarized.

Sensory, motor, and cognitive processes of the IPS

The parietal cortex is associated with a wide range of sensory, motor, and cognitive functions (Critchley, 1953). Because of its complex and multimodal responses, the parietal cortex is considered as part of the “tertiary association cortex” (Culham and Kanwisher, 2001). In particular, a variety of visuospatial tasks has been found to activate the parietal cortex such as hand reaching, grasping, saccades, attention orienting, mental rotation, and spatial working memory as well as guidance of actions yield activation (Culham and Kanwisher, 2001; Simon et al., 2002). These cognitive functions

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[10] The base-10 place-value structure is based on the position of each digit which determines the numerical value within the respective digit string without proportional aspects (i.e., base-10 place-value structure: e.g., $35.4 = 3 \times 10^1 + 5 \times 10^0 + 4 \times 10^{-1}$; Huber et al., 2014b).

partly share processes across domains, and thus, show overlapping activation in the parietal cortex while smaller sub-regions exhibit domain-specific activations (Humphreys and Lambon Ralph, 2015).

In particular, IPS and superior parietal lobule (SPL) are involved in a variety of tasks including top-down attention, numerical calculation, executive semantics, phonological tasks, and tool-praxis decisions (Humphreys and Lambon Ralph, 2015). Furthermore, IPS and SPL are specifically involved in the storage and manipulation of items held in working memory during goal-directed and executively demanding tasks (Humphreys and Lambon Ralph, 2015; Jonides et al., 1998). As these tasks are non-automatic, goal-directed and highly demanding, it was assumed that these brain regions support a general top-down processing system as part of a fronto-parietal executive system across domains (Cabeza, 2008; Corbetta and Shulman, 2002; Humphreys and Lambon Ralph, 2017, 2015).

Visual attention processes and reorienting spatial attention are widely considered to show a right hemispheric predominance (Arrington et al., 2000; Corbetta et al., 2000; Thiel et al., 2004). Also neuropsychological studies in patients with parietal lesions in the right hemisphere found deficits in attentional processes (Becker and Karnath, 2007; Heilman et al., 1985; Sturm et al., 2004), while motor attention has been shown to be linked to the left parietal cortex (Rushworth et al., 2003, 2001).

Additionally, the IPS is involved in suppression of task-irrelevant distractors (Wojciulik and Kanwisher, 1999) and response-selection processes (Göbel et al., 2004). Thus, in the parietal lobes processes are subserved, which are not specific for magnitude processing itself, but are necessary for or associated with the processing of numbers such as top-down attention, spatial representation, working memory, eye movements, and the guidance of actions (Culham and Kanwisher, 2001; Humphreys and Lambon Ralph, 2015).

Thus, previous research indicated that the IPS hosts a domain-general multi-demand system involving a variety of sensory, motor, and cognitive processes ranging from attentional processes to mental navigation as well as from pointing and grasping to number processing (e.g., Humphreys & Lambon Ralph, 2015; Humphreys & Ralph, 2017; Simon et al., 2002). Additionally, there is evidence that these different goal-directed processes interact as they all require a domain-general executive system (e.g., Hubbard, Piazza, Pinel, & Dehaene, 2005; Humphreys & Lambon Ralph, 2015). For instance, Knops and colleagues (2009) showed that brain circuits associated with spatial attention contribute to mental arithmetic. These results substantiate the notion that number processing co-opts parietal circuits involved in low-level sensorimotor tasks such as spatial attention and eye movements.

Furthermore, shared activation for grasping and pointing was observed in left IPS extending into superior parietal lobule (SPL) and postcentral sulcus (Simon et al., 2002). These motor tasks (i.e., grasping and pointing) also showed joint activation with visuospatial tasks such as saccades and attention orienting in bilateral SPL (Simon et al., 2004, 2002). Interestingly, overlapping activation was also observed with mental calculation, language, and saccades in the left posterior segment of the IPS beneath the angular gyrus (Simon et al., 2002). Thus, number processing and mental calculation does not only co-opt parietal circuits of low-level sensorimotor tasks, but also shares brain areas with other higher cognitive functions such as language. Importantly, these different cognitive processes share common features of executive demands (Humphreys and Lambon Ralph, 2017). As such, the IPS is not a brain region specifically dedicated to numerical cognition. Rather, the ability to process numbers and numerosities seems to involve number-unspecific processes such as top-down processes, spatial attention, working memory, as well as executive processes which are hosted in an intraparietal executive system across domains with more domain-specific areas surrounding it (Humphreys and Lambon Ralph, 2017).

The present study

Previous research focused either on the magnitude processing of symbolic (DeWolf et al., 2016; Ischebeck et al., 2009a; Jacob and Nieder, 2009b) or non-symbolic proportions (Jacob and Nieder, 2009a) or on the question whether symbolic and non-symbolic proportions share an intraparietal neural correlate for overall magnitude processing, irrespective of presentation format (Mock et al., 2018). However, it has not yet been investigated whether there is a joint neural correlate in intraparietal areas associated with above described domain-specific numerical and domain-general cognitive processes. A closer look at the results of our latest study (Mock et al., 2018) provides an indication that there may be such shared intraparietal processes not necessarily specific to overall magnitude processing: the shared neural correlate in the right IPS for overall magnitude processing of symbolic and non-symbolic proportions as reflected by the numerical distance effect was rather small (k = 46 voxels; Mock et al., 2018). Typically, activated clusters in IPS are considerably larger for processing natural numbers or proportions, irrespective of presentation format (e.g., Arsalidou & Taylor, 2011 for a review and meta-analysis). Thus, these larger clusters might reflect the involvement of further cognitive processes complementing magnitude processing. In fact, to operate on magnitude information of proportions (e.g., fractions, decimals, pie charts, and dot patterns), other rather domain-general cognitive processes such as attention, eye movements during the comparison, working memory, and mental rotation in non-symbolic formats might be required besides domain-specific numerical processes (e.g., magnitude). Furthermore, even though overall magnitude processing of symbolic and non-symbolic proportions elicited joint activation in the right IPS (Mock et al., 2018), it is still unclear whether the underlying neural processes to operate on this relative magnitude information are also shared, or at least similar. Another important question we tackle in the present study is how bipartite part-whole relations (e.g., fractions, pie charts, and dot patterns only) are processed at the neural level. The bipartite structure of these presentation formats requires relating their components (e.g., denominator and numerator of a fraction) to infer overall magnitude information, which may require additional domain-general cognitive processes to determine part-whole relations.

To pursue this issue, the present study took a two-step procedure. In a first step, we aimed at investigating whether there is a joint neural correlate for domain-specific numerical and domain-general processes in proportion processing at the whole-brain level. In a second step, we investigated the processing of part-whole relation in more detail by contrasting conditions requiring processing of part-whole relations (i.e., fractions, dot patterns, and pie charts) to decimals, which do not require part-whole but base-10 processing. Additionally, based on the results of the first step, we also pursued the question whether possibly shared activation patterns also indicate shared underlying neural processes in the parietal cortex. It is important to note that the current work and Mock et al. (2018) report on complementary aspects of the same dataset and that the current results reflect analyses of both domain-specific numerical as well as domain-general processes as compared to the specific processing of overall proportion magnitude in the IPS (as reflected by the numerical distance effect) as evaluated by Mock et al. (2018).

We employed four different magnitude comparison tasks with symbolic (e.g., fractions and decimals) and non-symbolic proportions (e.g., dot patterns and pie charts), respectively. As previous studies showed an involvement of bilateral parietal regions and the prefrontal cortex (PFC) during processing of symbolic and non-symbolic proportions, we expected a shared neural correlate for all four presentation formats in this fronto-parietal network including IPS. First, we identified joint intraparietal activation using a conjunction analysis on the whole-brain level. Second, and most importantly, as DeWolf and colleagues (2016) found that symbolic part-whole relations (e.g., fractions) yielded an activation pattern distinct from that observed for numbers complying with the base-10 structure, we examined the contrast between proportions reflecting bipartite part-whole relations (i.e., fractions, dot patterns, and pie charts) and decimals on a whole-brain level. This way, we were able to evaluate activation specific to part-whole processing without the interference of base-10 processing.

Furthermore, in doing so we extended the scope of previous research (DeWolf et al., 2016) by including non-symbolic presentation formats.

To further evaluate proportion processing specifically in the parietal cortex, the resulting clusters of the conjunction analysis were taken as regions of interest (ROIs) for which the respective BOLD signal change was evaluated. Finally, possible differences between processing part-whole relations versus decimals were evaluated by a representational similarity analysis (RSA) differentiating the similarity of the intraparietal BOLD response for the different presentation formats in the bilateral IPL.

7.2 Results

Behavioral results

Mean speed of participants in the four conditions for dot patterns, fractions, pie charts, and decimals, respectively, was: M_{dots} = 0.57 (*SE* = 0.04) items/sec, $M_{fractions}$ = 0.57 (*SE* = 0.03) items/sec, M_{pies} = 0.85 (*SE* = 0.04) items/sec, and $M_{decimals}$ = 1.10 (*SE* = 0.03) items/sec.

In the next step, a univariate ANOVA with speed as the dependent variable and presentation format (dot patterns, pie charts, fractions, and decimals) as a fixed factor was conducted to compare the effect of presentation format on speed. The main effect was highly significant [presentation format: $F(3, 104) = 48{,}57$, $p < .001$, $\eta_G^2 = .584$], indicating that participants' speed differed between presentation formats. Post-hoc comparisons revealed that except for the difference between dot patterns and fractions ($p = 1$) speed differed significantly from each other in all presentation formats (all $p < .001$). Figure 7.1A gives an overview for speed data.

Moreover, mean accuracy in the four conditions for dot patterns, fractions, pie charts, and decimals, respectively, were: M_{dots} = 70.7% (*SE* = 2.75%), $M_{fractions}$ = 77.7% (*SE* = 2.77%), M_{pies} = 91.0% (*SE* = 0.9%), and $M_{decimals}$ = 98.0% (*SE* = 1.0%). Again, the univariate ANOVA revealed significant main effect of presentation format [$F(3, 104) = 36.02$, $p < .001$, $\eta_G^2 = .510$]. Post-hoc comparisons indicated that the difference in accuracy was significant for all presentation formats ($p < .001$) except the difference between pie charts and decimals ($p = .082$) and between dot patterns and fractions ($p = .090$). Accuracy for the different presentation formats is shown in Figure 7.1B.

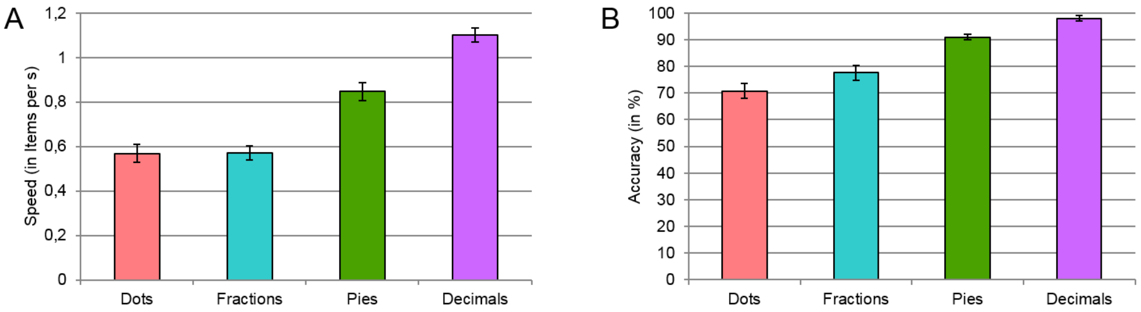

Figure 7.1: A Speed and B accuracy in the four conditions (dot patterns, fractions, pie charts, and decimals).

Imaging results

Whole-brain conjunction analysis

The conjunction analysis across the four conditions (e.g., fractions, decimals, dot patterns, pie charts) revealed significant joint activation in visual occipital areas (e.g., lingual gyrus, calcarine gyrus, inferior occipital gyrus), bilateral thalamus and supplementary motor areas. Importantly, joint activation was also found in bilateral inferior parietal cortex, close to its junction with the IPS (see Table 7.1 and Figure 7.2).

Table 7.1: Joint activations across the four conditions (i.e., fractions, decimals, dot patterns, pie charts) as revealed by the conjunction analysis. Activations were thresholded at a whole-brain FWE *p*-value of < .05 with a cluster size of *k* = 10 voxels.

Contrast	Brain region	MNI (x, y, z)			*k*	*t*
Conjunction	LH inferior parietal lobule	-45	-32	43	40	6.08
	RH inferior parietal lobule	51	-25	48	28	5.74
	LH thalamus	-22	-27	-3	39	11.73
	RH thalamus	23	-27	-3	42	10.21
	RH supplementary area	1	6	53	56	7.86
	RH lingual gyrus	16	-97	-8	3637	25.15
	LH lingual gyrus*	-10	-90	15		17.67
	RH calcarine gyrus*	13	-90	3		17.24
	LH calcarine gyrus*	-5	-90	-5		18.17
	LH middle occipital gyrus*	-22	100	3		20.37
	RH middle occipital gyrus*	16	102	8		19.57
	LH inferior occipital gyrus*	-22	-95	10		22.95
	RH inferior occipital gyrus*	31	-85	10		16.11

Abbreviations: *k* = cluster size; LH = left hemisphere; MNI: Montreal Neurological Institute; RH = right hemisphere; FWE-corrected *p*-value < .05, cluster size *k* = 10 voxels; *t* = *t*-value. * Minor maximum.

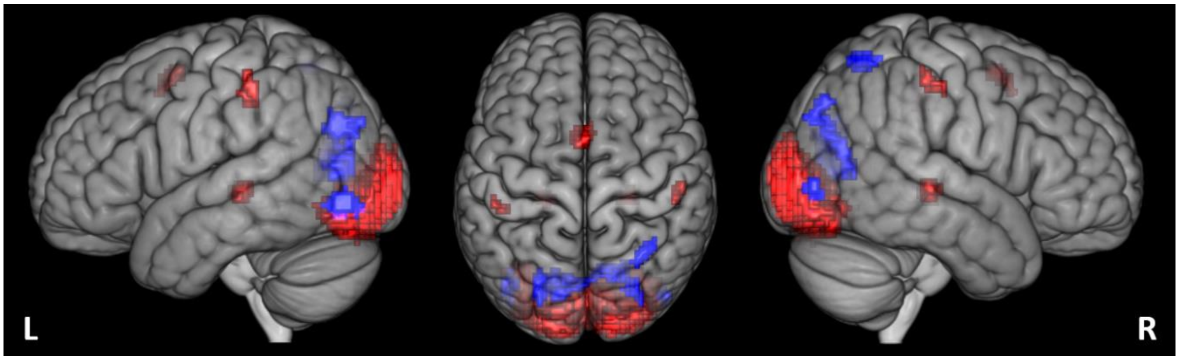

Figure 7.2: Significant joint activation for proportion processing across the four conditions (e.g., fractions, decimals, dot patterns, pie charts) is given in red. The blue clusters indicate significant activation specific to overall magnitude processing as reflected by the numerical distance effect across the four presentation formats in a nearby, but different brain region (Mock et al., 2018). Activations were thresholded at a whole-brain FWE-corrected *p*-value of < .05.

Contrast between part-whole relations and decimals

The contrast between the bipartite part-whole relations (i.e., fractions, dot patterns, and pie charts) and decimals revealed significant activation in bilateral inferior parietal lobule including bilateral IPS, areas in bilateral middle frontal gyrus, bilateral SMA, and bilateral insula (see Table 7.2 and Figure 7.3).

Table 7.2: Activations for part-whole processing as revealed by the contrast part-whole (i.e., fractions, pie charts, and dot patterns) vs. decimals. Activations were thresholded at a whole-brain FWE *p*-value of < .05 with a cluster size of *k* = 10 voxels.

Contrast	Brain region	MNI (x, y, z)			*k*	*t*
Part-whole	RH Inferior parietal lobule (hIP2)	46	-40	50	1825	10.99
vs. decimals	RH Inferior parietal lobule (IPL)*	51	-37	53		10.59
	RH Superior occipital gyrus*	28	-65	40		9.53
	RH Superior parietal lobule*	26	-67	40		9.34
	LH Inferior parietal lobule (hIP3)	-35	-50	48	1164	8.48
	LH Inferior parietal lobule (IPL)*	-47	-37	48		8.36
	LH Middle occipital gyrus*	-25	-65	38		8.34
	LH Inferior parietal lobule (hIP1)*	-32	-47	43		8.30
	RH Middle frontal gyrus	43	36	20	633	10.70
	RH Inferior frontal gyrus*	48	13	30		8.96
	RH Supplementary motor area	6	26	45	267	8.96
	LH Supplementary motor area*	-7	21	45		8.11
	RH Insula	33	28	-3	169	10.46
	RH Middle frontal gyrus	31	11	60	166	7.35
	LH Precentral gyrus (Area 44)	-42	3	33	153	6.71

LH Insula	-32	21	-3	121	8.49
LH Inferior frontal gyrus (Area 45)	-47	28	30	88	6.55
LH Middle orbital gyrus	-42	46	-3	68	6.45
RH Middle orbital gyrus	38	53	-3	46	6.34

Abbreviations: *k* = cluster size; LH = left hemisphere; MNI: Montreal Neurological Institute; RH = right hemisphere; FWE-corrected *p*-value < .05, cluster size *k* = 10 voxels; *t* = *t*-value. * Minor maximum.

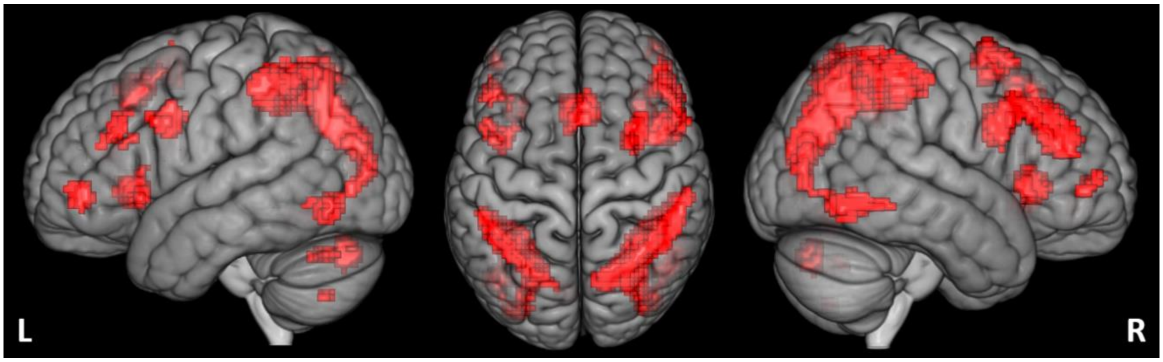

Figure 7.3: Contrast between part-whole proportions (i.e., fractions, dot patterns, and pie charts) and decimals (part-whole – decimals). Significant activation depicts part-whole relation processing without base-10 related processing. Activations were thresholded at a whole-brain FEW-corrected *p*-value of <.05.

Signal change within IPL ROIs

Mean percent signal change of the four presentation formats for bilateral IPL clusters found in the conjunction analysis (see 2.2.1) is given in Figure 7.4. We compared the percent signal change by running a 4 × 2 ANOVA with factors presentation format (dot patterns, pie charts, fractions and decimals) and hemisphere (left and right). Only the main effect of presentation format was significant, $F(2.67, 61.35) = 18.51$, $p < .001$, $\eta_G^2 = .167$. In contrast, the main effect of hemisphere as well as the interaction between presentation format and hemisphere was not significant; hemisphere: $F(1, 23) = 2.98$, $p = .098$, $\eta_G^2 = .184$, and presentation format × hemisphere: $F(2.50, 57.58) = 2.03$, $p = .130$, $\eta_G^2 = .006$. Post-hoc comparisons revealed that percent signal changes differed significantly between presentation formats (all $p < .04$) except for percent signal changes for dot patterns and pie charts ($p = .836$).

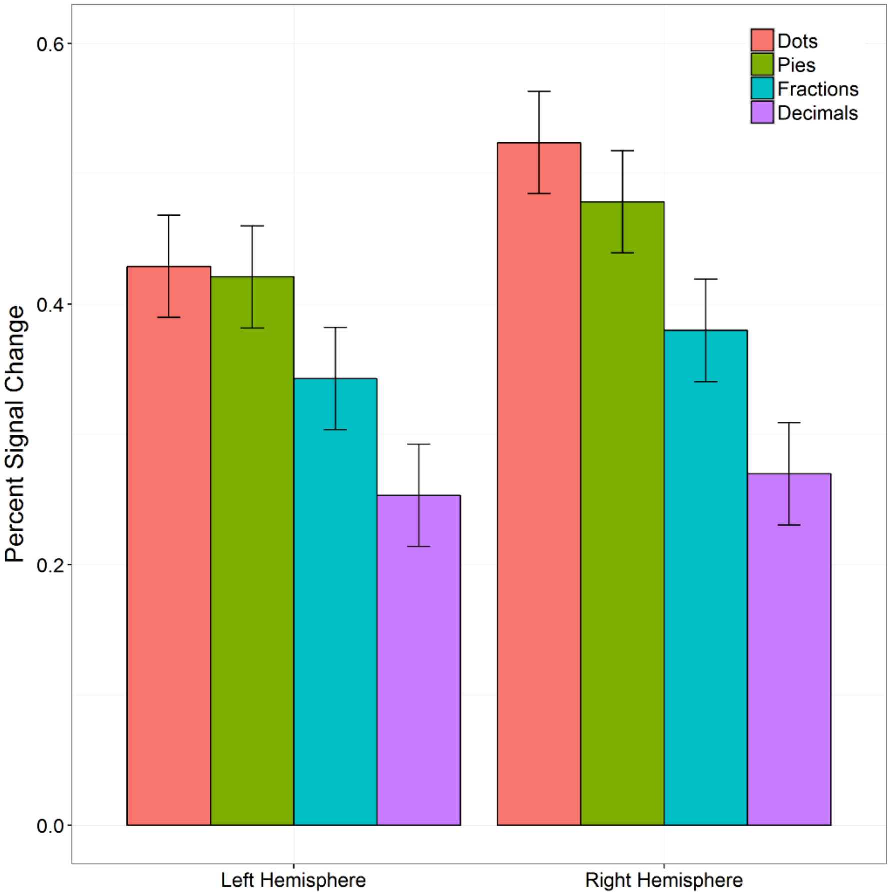

Figure 7.4: Percent signal change of the four presentation formats of the clusters in the inferior parietal cortex for left and right hemisphere. Error bars indicate +/- 1 standard error of the mean.

Representational similarity

Descriptively, the resulting RSMs for left and right hemispheres were very similar (see Figure 7.5). We observed that the activation pattern for dot patterns was very similar to the one for fractions (LH: sim = 0.93; *SD* = 0.07; RH: sim = 0.92; *SD* = 0.06) and pie charts (LH: sim = 0.88; *SD* = 0.10; RH: sim = 0.89; *SD* = 0.09), whereas the activation pattern for decimals differed more from dot patterns (LH: sim = 0.77; *SD* = 0.17; RH: sim = 0.74; *SD* = 0.16). Furthermore, the activation pattern for pie charts was more similar to the activation pattern for decimals (LH: sim = 0.86; *SD* = 0.13; RH: sim = 0.83; *SD* = 0.10). Moreover, the similarity of the activation patterns for pie charts and fractions (LH: sim = 0.84; *SD* = 0.12; RH: sim = 0.84; *SD* = 0.08) was in the same range as the similarity between the one for pie charts and the other presentation formats. However, activation patterns for decimals and fractions differed more strongly (LH: sim = 0.74; *SD* = 0.19; RH: sim = 0.70; *SD* = 0.18).

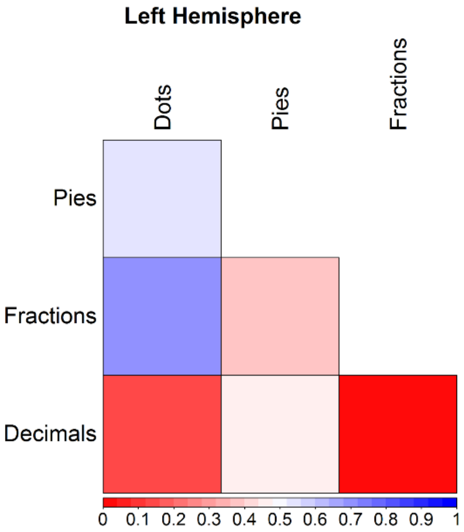

Figure 7.5: Min-max normalized Representational Similarity Matrix for the four different notation formats with 1 being most similar.

The resulting dendrograms of the hierarchical cluster analysis for left and right hemisphere are shown in Figure 7.6. Comparable to the RSM, it indicated that activation patterns for fractions, dots, and pie charts were very similar, whereas activation patterns of decimals differed from the other presentation formats.

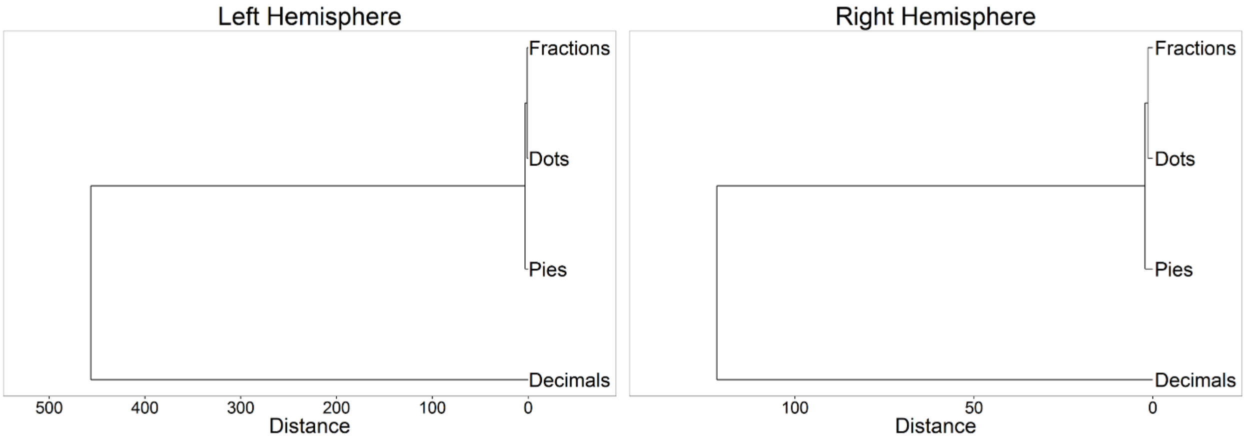

Figure 7.6: Dendrograms for left and right hemisphere of the agglomerative hierarchical cluster analysis on the mean z-standardized β estimates for the four different notation formations. Distance indicates the Euclidean distance with lower distance being more similar.

7.3 Discussion

The present study aimed at investigating whether there is a shared neural substrate in the IPL for domain-specific numerical as well as domain-general aspects of processing proportions beyond processing overall magnitude (as reflected by the numerical distance effect, cf. Mock et al., 2018). It is important to note that we already reported complementary aspects specific to overall magnitude processing of this dataset in Mock et al. (2018). Here, we aimed at evaluating the processing of proportions more broadly and part-whole relations in particular. Additionally, we were interested in whether shared neural activation patterns in the parietal cortex may also indicate shared underlying neural processes across different notations. To explore the cognitive demands during proportion processing in bilateral IPL in more detail, we applied an analysis of the BOLD signal change and a complementary RSA based on clusters of joint parietal activation identified in our conjunction analysis. In the following, we will first discuss the joint neural substrate found for processing proportions and part-whole relations in particular before we elaborate on our findings on shared underlying neural processes within the IPL.

A joint intraparietal neural substrate for processing of proportions

Our observation of joint bilateral IPL activation is in line with a recent meta-analysis by Sokolowski and colleagues (2017) who reported joint activation in bilateral IPL for the processing of symbolic and non-symbolic natural numbers. Importantly, our results extend this previous research because we used symbolic and non-symbolic proportions instead of integers and numerosities only. This substantiates the idea of IPL to be crucially involved in number processing in general.

Yet, the joint neural correlate found in our data may not exclusively reflect number magnitude processing (Sokolowski et al., 2017). On the other hand, we also do not wish to claim that the joint activation found in bilateral IPL exclusively reflects domain-general processes without any aspect of magnitude processing. Instead, the observed IPL activation may well reflect processing and operating on number magnitude information. However, when investigating intraparietal processing specific to overall magnitude processing within the very same data set in a previous study (Mock et al., 2018, reflected by the numerical distance effect), we observed joint activation for overall magnitude processing of these presentation formats in a small cluster in right IPS only (MNI: 31, -60, 60; k = 46 voxels). Thus, the core area for the processing of overall relative magnitude differed from the region we found in the present study (see also Figure 7.2). Therefore, we suggest that the neural overlap found in the present study might rather reflect shared task demands for all four presentation formats such as visuo-spatial and top-down attention (Humphreys and Lambon Ralph, 2017), estimation, summation, and calculation processes (Castelli et al., 2006; Holloway et al., 2010; Piazza et al., 2006; Venkatraman et al., 2005), working memory during maintenance and manipulation of the to-be-compared items (Humphreys and Lambon Ralph, 2015; Jonides et al., 1998), eye movements (Knops et al., 2009; Simon et al., 2004, 2002), or response-selection (Göbel et al., 2004).

Although symbolic and non-symbolic proportions used in this study were conceptually distinct (part-whole vs. base-10), we nevertheless found a joint neural substrate in the parietal cortex indicating shared processes. Unfortunately, we are not able to further distinguish the processes involved on the basis of our design. However, we speculate that these processes might include domain-general visuo-spatial and top-down attentional processes, and working memory (Culham and Kanwisher, 2001; Göbel et al., 2004; Humphreys and Lambon Ralph, 2017, 2015; Simon et al., 2002) but also more domain-specific estimation, summation, and calculation processes (Castelli et al., 2006; Holloway et al., 2010; Piazza et al., 2006; Venkatraman et al., 2005) necessary to compute the relative magnitude of the given proportions. This is in line with the assumption of Humphreys and Lambon Ralph (2015; 2017) who proposed a domain-general executive system in the IPS and SPL for shared non-automatic top-down processes during demanding, goal-directed tasks. Overall proportion magnitude, however, may be processed in the right IPS (Mock et al., 2018), which might correspond to a more domain-specific subregion close to this domain-general executive system in a nearby, but different brain area. As working memory processes are also associated with frontal brain areas, previous studies additionally reported activation in PFC during processing symbolic fractions and non-symbolic proportions (Ischebeck et al., 2009a; Jacob and Nieder, 2009a, 2009b). Hence, we also expected a joint fronto-parietal network being involved in the processing of symbolic and non-symbolic proportions. However, we only observed activation in the dorsolateral PFC for the processing of fractions, dot patterns and pie charts, but not for the processing of decimals (see Appendix for the whole-brain analysis of the four presentation formats against baseline, respectively). As such, the results of our conjunction analysis did not reveal joint prefrontal activation. This suggests that fractions and non-symbolic proportions such as pie charts and dot patterns may be processed differently from decimals, as only the former activated a fronto-parietal network whereas the latter did not (see Appendix; for similar results on differences in processing fractions and decimals, see DeWolf et al., 2016).

Neural processing of part-whole relations

Fractions, dot patterns, and pie charts reflect bipartite part-whole relations. In particular, the bipartite structure of these presentation formats requires relating their two parts to infer the respective relative magnitude information. That is, the relation between the two proportional components determines overall relative magnitude. In contrast, decimals do not require these relating processes or additional computational steps and simply reflect their magnitudes based on their base-10 structure. To disentangle part-whole from base-10 processing, we evaluated the contrast between part-whole proportions and decimals. Thereby, we were able to investigate part-whole relation processing without interfering symbol-to-referent mapping of base-10 notations.

We found large activated clusters in bilateral IPL extending to bilateral occipital gyrus, bilateral SMA, bilateral insula, as well as clusters in bilateral middle and inferior frontal gyrus. Parts of the activation found in bilateral IPL (i.e., right IPS) have been associated with magnitude-specific processing of proportions previously (Mock et al., 2018). However, as these brain regions also seem to host an intraparietal domain-independent system of executive processes, the observed activation might also indicate the involvement of top-down processes, spatial attention, working memory, and other executive processes (e.g., Fias et al., 2013; Humphreys & Lambon Ralph, 2017). The activation of bilateral inferior frontal gyri also supports the idea of an involvement of top-down and working memory processes. Activation in these brain areas was associated with visual working memory (e.g., Song and Jiang, 2006), higher cognitive monitoring such as choosing, comparing, or judging and manipulation of information (e.g., Christoff et al., 2000; Ranganath et al., 2003), procedural complexity (e.g., Delazer et al., 2003; Simon et al., 2002), as well as attentional processes (e.g., Ischebeck et al., 2009b). Furthermore, the inferior frontal gyri also seem to underlie strategy choice and planning in mathematical processes (e.g., Arsalidou and Taylor, 2011; Dehaene and Cohen, 1997). Additionally, bilateral insula was associated with the execution of responses (e.g., Huettel et al., 2001) and goal-directed motivated behavior (e.g., Uddin & Menon, 2009). Thus, the broad activation of a fronto-parietal pattern of brain areas may suggest the involvement of domain-general cognitive processes such as working memory, top-down attentional and executive processes, as well as strategy choice that go beyond pure magnitude processing.

Interestingly, joint activation of dorsolateral frontal cortex including inferior and middle frontal gyrus, insula, precentral gyrus, and SMA, as well as areas in and around the IPS was interpreted to reflect a so-called multiple demand system (MD, see Duncan, 2010; Fedorenko et al., 2013) or an extrinsic mode network (EMN, see Hugdahl and colleagues, 2015). The MD system is associated with diverse cognitive and executive control demands including perception, response selection, language, memory processes, problem solving, and task novelty independent of the actual task at hand (Duncan, 2013, 2010; Fedorenko et al., 2013). The EMN extends the concept of the MD suggesting a common activation pattern structure and up-regulating during task processing, independent of the specific cognitive task at hand (Hugdahl et al., 2015). For instance, EMN was shown to be activated by distinct cognitive tasks (e.g., spatial working memory, response inhibition, impulse control, executive function, mental rotation, and arithmetic) and responds to focused attention, goal maintenance, strategy selection, working memory and performance monitoring (Fedorenko et al., 2013; Hugdahl et al., 2015). Hence, brain areas associated with MD and the EMN show a broad functional generality.

Importantly, the brain regions we found for part-whole relation processing are strikingly similar to the ones comprised by the MD and the EMN. This further supports the notion of domain-general processes being involved in the processing of part-whole relations, not only on the whole-brain level but also specifically in parietal brain regions. It is important to note, however, that we do not suggest that part-whole relations are exclusively processed by domain-general networks. Instead, like all human cognition, this processing is accomplished by a combination of domain-specific regions like the parts of the IPS for number magnitude processing (Mock et al., 2018) and domain-general cognitive and neural mechanisms (Duncan, 2013; Fedorenko et al., 2013; Hugdahl et al., 2015). Thus, for the case of processing part-whole relations MD and EMN are complemented by highly specialized brain regions. However, the question remains why we find MD and EMN activation for part-whole relation processing, but not for processing proportions in general including decimals. Hugdahl and colleagues (2015) argued that the EMN is sensitive to learning and experience, which means that overlearned tasks do not activate the EMN (Hugdahl et al., 2015). As magnitude processing of decimals is very similar to the processing of other multi-digit numbers (when skipping the leading 0) adults are confronted permanently with in everyday life, we suggest that decimals may be overlearned as compared to symbolic or non-symbolic proportions. Hugdahl and colleagues (2015) further suggested that the EMN follows a threshold effect which varies depending on task novelty (Hugdahl et al., 2015). This way, the absence of MD and EMN in our conjunction analysis can be explained by the fact that processing of decimals reduces the experience of novelty, and thus, down-regulates the EMN. In contrast, when task novelty is high, which was apparently the case in the part-whole relation tasks, EMN is up-regulated complementing highly domain-specific brain mechanisms.

Cognitive demands during proportion processing in bilateral IPL

When analyzing BOLD signal change in the bilateral IPL ROIs identified by the conjunction analysis, we only found a main effect for the four presentation formats. There was no difference between hemispheres and also no interaction although left parietal cortex was recently suggested to be associated rather with the processing of symbolic numbers whereas right parietal cortex with the processing of non-symbolic numerosities (Cappelletti et al., 2010, 2009; Holloway et al., 2010;

Sokolowski et al., 2017). However, previous research on this lateralization mainly focused on number magnitude processing, while we investigated proportion processing beyond overall magnitude processing. This might also indicate that the BOLD signal change found in our data rather reflects other cognitive processes necessary for the processing of symbolic and non-symbolic proportions than just overall magnitude processing.

The highest signal change was found for both non-symbolic presentation formats (e.g., dot patterns and pie charts), probably indicating higher demands on visuo-spatial attention as well as maintenance and manipulation of the respective items in working memory. In particular, the processing of proportional dot patterns might require more eye movements between the dots for individuation and summation of non-symbolic items (Holloway et al., 2010) whereas the processing of pie charts might rather involve mental rotation strategies (Alivisatos and Petrides, 1997; Jordan et al., 2001). Regardless of whether summation or mental rotation strategies are used to finally operate on the magnitude of those non-symbolic formats, the task is highly demanding and visuo-spatial attention is highly required. This assumption is further substantiated by additional activation observed in bilateral frontal eye fields (FEF) and posterior superior parietal lobule (PSPL) for both of these non-symbolic presentation formats as these regions are typically associated with eye movements (see Appendix A3 and A4; Knops et al., 2009). Additionally, activation in PFC reflect the involvement of executive control, working memory and attentional processes sending top-down signals to IPL (Humphreys and Lambon Ralph, 2015).

Furthermore, signal change for fractions was higher compared to decimals. This might indicate higher attentional loads as well as working memory demands during additional computational steps to access overall magnitude information of fractions (Mock et al., 2018). Moreover, eye movements between the two fractions or between their numerators and denominators might lead to higher visuo-spatial attention loads. In fact, for the processing of fractions we also observed additional activation in FEF and PSPL which are typically associated with eye movements (Knops et al., 2009) and prefrontal activation reflecting top-down attentional and working memory processes (see Appendix A1; Humphreys & Lambon Ralph, 2015).

In contrast, no additional computations and only low attentional demands are required while processing decimals. Rather, a simple symbol-to-referent mapping might seem plausible for decimals as they directly reflect number magnitudes (Holloway et al., 2010). This idea is corroborated by activation in areas subserving these processes such as left angular gyrus and superior and middle temporal gyrus, which can be observed for decimals using a slightly less conservative correction for the fMRI data (p < .001, uncorrected) than reported in the Appendix A2 (p < .05, FWE-corrected). In particular, these brain regions are rather associated with bottom-up and automatic processes which further supports the assumption of a direct symbol-to-referent mapping (Humphreys and Lambon Ralph, 2015). Thus, in contrast to the bipartite structure of the other presentation formats decimals do not seem to reflect proportional aspects in the same way.

Importantly, activation in parietal brain regions was previously associated with tasks requiring additional attention due to higher levels of difficulty (Culham et al., 1998; Culham and Kanwisher, 2001; Humphreys and Lambon Ralph, 2017; Shuman and Kanwisher, 2004). Thus, parietal activation during numerical tasks might also be driven by task difficulty to some degree. However, in the present study the signal change induced by proportion processing did not exactly resemble the pattern found in the behavioral data. That is, the difficulty pattern found in speed and accuracy differed from the pattern observed for signal change in the bilateral IPL. Speed was lowest for fractions and dot patterns. Yet, comparing pie charts led to faster responses, while participants achieved highest speed when comparing decimals. Additionally, accuracy in our data was highest for decimals and pie charts, whereas accuracy for fractions and dot patterns was similarly low. As increasing response times and error rates might indicate influences of task difficulty, these behavioral results seem to reflect the difficulty in operating on magnitude information between the different presentation formats. However, the signal change analysis revealed a different pattern. Furthermore, previous studies found activations in the intraparietal cortex for either passive listening to number words (Klein et al., 2010) or passive viewing of symbolic numbers versus letters and colors (Eger et al., 2003). This indicates that intraparietal activations can be associated, at least partially, with number processing independent from difficulty level. Thus, our results cannot be attributed to differences in difficulty exclusively.

Shared underlying neural processes of symbolic and non-symbolic proportions

Although fractions, dot patterns, pie charts, and decimals reflect conceptually different properties (part-whole vs. base-10), they activated a joint neural correlate as reflected by the conjunction analysis. However, a joint neural substrate does not necessarily implicate one common underlying process. Therefore, we conducted an RSA to gain more fine-grained results because this analysis evaluates similarities in the activation patterns of the four presentation formats.

The RSA revealed that the patterns of neural activations elicited by the part-whole relations (i.e., fractions, dot patterns, and pie charts) were very similar. That is, voxels in bilateral IPL responded very similarly when processing symbolic fractions as well as non-symbolic dot patterns and pie charts.

Thereby, our results indicate a dissociation between the patterns of neural activation elicited by decimals and the other presentation formats which further substantiates our contrast analysis. Furthermore, this is in line with the results of DeWolf and colleagues (2016) who observed that the activation pattern for fractions differed systematically from that of decimals and integers within the parietal cortex. Whereas the latter two number formats were hardly distinguishable, DeWolf and colleagues (2016) were able to clearly differentiate activations for fractions. Thus, the major notations for symbolic proportions (i.e., fractions and decimals) seem to draw on distinct neural processes even when they express the same magnitude (e.g., 2/5 and 0.4). The present results indicate that fractions share an underlying neural process with proportional dot patterns and pie charts, whereas the neural processing of decimals differs. A plausible explanation for our finding is that the underlying neural processing of fractions, dot patterns and pie charts reflects the bipartite structure of proportional part-whole relations. In contrast, decimals simply and directly reflect number magnitudes in a base-10 notation (e.g., see Huber et al., 2014b) and do not require the additional processing of proportional aspects. Thus, the structure of proportions (part-whole vs. base-10) seems to determine their underlying neural processing. Depending on the structure task demands might differ which, in turn, seems to change the respective activation patterns. This is in line with Humphreys and Lambon Ralph (2015) who suggested that parietal organization is not split by domain-specific tasks but rather meets the requirements of demanding tasks by adjusting respective neurocomputations. While performing a task, the respective activation pattern within parietal cortex might change due to different task demands (Humphreys and Lambon Ralph, 2015; see also Hugdahl et al., 2015 for a similar threshold effect in the EMN). Relating this to our data, pie charts, dot patterns, and fractions might have elicited similar neurocomputations within the IPL because of their structural similarity (i.e., bipartite part-whole relation), which, in turn, is reflected by the reported RSA pattern. In contrast, neurocomputations required for processing decimals on the neural level might differ as they do not reflect this bipartite part-whole relation.

Limitations

We are well aware that the current study is only a first step towards a more comprehensive understanding of the underlying processes in proportion processing. Thus, several aspects need to be considered when interpreting the results.

First, the design of the present study does not allow to further differentiate between domain-specific and domain-general mechanisms involved in proportion processing as the task at hand was a magnitude comparison task. However, in our view, activation patterns found for proportion processing in the present study do not reflect magnitude processing exclusively because we observed a core area for overall magnitude processing reflected by the numerical distance effect exclusively in the right IPS for the same data set (Mock et al., 2018). Thus, although magnitude information might be processed as well in the present study, additional activation found here might reflect the additional involvement of more domain-general processes associated with proportion processing. Although our interpretation has to remain speculative, our findings nevertheless fit well with the literature. Yet, to disentangle this issue, future research is needed in which it would be desirable to specify the suggested domain-general processes.

Second, it needs to be noted that the pattern of our RSA might be influenced by task difficulty. In fact, participants responded more accurate and faster to decimals. In turn, they spent more time viewing the scrambled mask consisting of visual noise than doing the actual proportion magnitude comparison as compared to the other presentation formats. Furthermore, as we used a block design attentional demands might be different between an easy block (e.g., comparing decimals) and a more difficult block (e.g., comparing dot patterns). In turn, this might have led to lower correlations in the RSA. However, usually influences of task difficulty are also reflected in the amplitude of fMRI signal change (Culham et al., 2001; Ress et al., 2000). In line with above argument, signal change was lowest for decimals. Nevertheless, the pattern found for signal change associated with the other presentation formats differed from the pattern found in the RSA as the amplitude in signal change was highest for the two non-symbolic formats. Thus, while we cannot fully exclude influences of task difficulty in the RSA pattern, we suggest that the RSA does at least not exclusively reflect task difficulty.

7.4 Conclusion

Proportion processing beyond overall magnitude processing elicited activation in frontal, parietal and occipital brain regions including bilateral IPL. However, observed activation in bilateral IPL, an area typically associated with number magnitude processing, did not reflect processing of overall proportion magnitude in our study. In fact, a shared neural substrate for the processing of abstract relative magnitude was observed in a nearby, but different brain area (i.e., right IPS) in a different analysis on the very same data set (Mock et al., 2018; see also Figure 7.2). Thus, the activation found in the present study does not necessarily reflect overall magnitude processing. Nevertheless, the shared neural correlate for proportion processing indicates common cognitive processes in a top-down executive parietal system. These processes might include visuo-spatial and top-down attention, estimation and summation processes, working memory, response-selection, and additional part-whole computations in the bilateral IPL for computing actual relative magnitude as well as relating and integrating the to-be-compared proportions.

Investigating processing of part-whole relations, we found wide-spread activation in fronto-parietal brain areas. This substantiates the involvement of domain-general cognitive processes in part-whole processing such as working memory, top-down attentional and executive processes, as well as strategy choice that go beyond magnitude processing. Thus, processing part-whole relations seems to be accomplished as an interplay of domain-specific (Mock et al., 2018) *and* domain-general cognitive and neural processes (Duncan, 2013; Fedorenko et al., 2013; Hugdahl et al., 2015) that complement each other.

The dissociation between part-whole relations (i.e., fractions, dot patterns, and pie charts) and decimals was substantiated by an additional RSA. Thus, although processing fractions, decimals, dot patterns, and pie charts elicited joint neural activation, the underlying neural processes seemed to be different depending on the structure of the respective proportion (i.e., part-whole vs. base-10). Thus, underlying structural differences of the notations seem to lead to distinct underlying neural processes.

7.5 Materials and Methods

Participants

Participants were 24 right-handed university students who participated voluntarily (13 females, mean age = 23.2 years; *SD* = 2.99 years). Participants gave their written consent according to the protocol of the local Ethics Committee of the Medical Faculty of the University of Tuebingen after being informed about the experimental procedure. All participants reported no previous history of neurological or psychiatric disorders and normal or corrected to normal vision. Participants received monetary compensation.

Procedure

Four different presentation formats of proportions were used in this study: fractions, decimals, pie charts, and dot patterns. Proportion processing was investigated by means of blocked magnitude comparison tasks (i.e., fractions, decimals, pie charts, and dot patterns). Proportions were presented pseudo-randomly in 24 blocks (six blocks per condition) consisting of one practice trial and four critical trials (120 trails in total: 24 practice and 96 experimental trials).

At the beginning of each block, a cue was presented for 500ms indicating which proportion type had to be compared in the next five trials. The cue was the fraction 1/4 shown in the respective presentation formats in the center of the screen against a grey background. Afterwards, a black screen was presented for 4,000 ms. Subsequently, trials started with a black fixation cross against a grey background for 500 ms, followed by the presentation of the to-be-compared proportion stimuli for up to 5,000 ms. Participants had to respond within this time frame by pressing one of two MRI compatible response buttons with either their left or right thumb indicating that either the left or the right proportion was larger, respectively. When participants responded faster than the given 5,000 ms, a mask consisting of visual noise (blue, yellow, and grey pixels) was presented for the remaining time. Then the next trial started. The procedure of the beginning of a block is shown in Figure 7.7. At the end of each block, a black screen was presented for 6,000 ms.

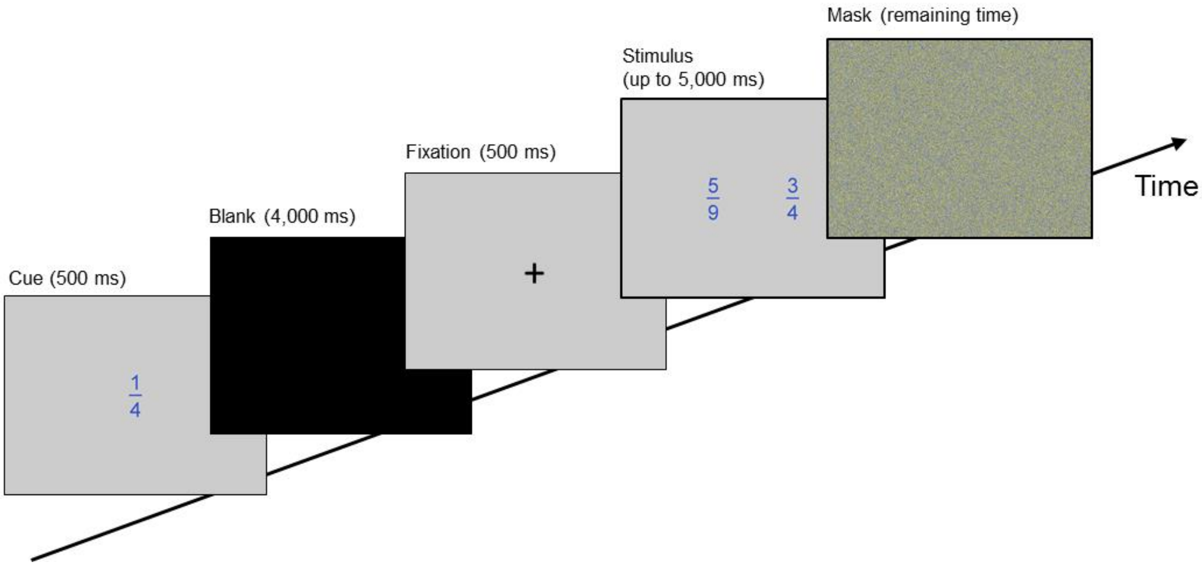

Figure 7.7: Experimental procedure at the beginning of each block (i.e., one out of five trials).

Stimuli

Proportions (i.e., fractions, decimals, pie charts, and dot patterns) were presented in pairs (see Figure 7.8). The magnitude of the first proportion ranged from 0.13 to 0.86 and the second proportion from 0.22 to 0.89.

Symbolic fraction items were generated first and then converted into the other presentation formats. Numerators of the fractions ranged from 1 to 8 and denominators from 2 to 9. Fractions were constructed such that in half of the items the comparison of numerators and denominators was either congruent or incongruent with the comparison of overall fraction magnitude. For congruent trials, separate comparisons of numerator and denominator magnitudes yielded the same answer as the comparison of the overall magnitudes of fraction pairs (e.g., 1/6 < 3/8 with 1 < 3 and 6 < 8). In contrast, separate comparisons of numerator and denominator magnitudes yielded opposing answers as compared to the overall magnitude of the fractions in incongruent trials (e.g., 4/7 < 2/3, but 4 > 2 and 7 > 3). Thus, participants were not able to solve the task correctly, when relying on the magnitude of numerators or denominators only. We then constructed decimals by dividing numerators by denominators and rounding the result to two digits after the decimal point. Decimals and fractions were presented in blue (font type: Arial; font size: 80; RGB-values: 53, 85, 204) against a grey background (RGB-values: 204, 204, 204). One fraction was located on the left side (x/y-coordinates: 356 / 384 px), whereas the other one was located on the right side (x/y-coordinates: 668 / 384 px) of the screen (screen resolution: 1024 × 768 px).

Dot patterns were drawn in the center of the left and the right side of the screen on an invisible rectangular area of size 491 × 363 px. Location of dots varied randomly in these invisible rectangular areas. Dot patterns were colored according to the fractions they denoted using blue (same blue as for fractions) and yellow (RGB-values: 203, 187, 0) against a grey background (same grey as for fractions and decimals). For instance, the dot pattern of 4/7 was drawn by coloring 4 dots in blue and 3 dots in yellow (and thus, 4 out of 7 dots were colored in blue). Diameter of dots varied randomly from 21 px to 98 px. To ensure that participants cannot rely on the proportion of the sum of visual areas when comparing the dot patterns, the sum of yellow and blue areas of the dots across the two dot patterns, which had to be compared, was equated.

Pie charts were drawn by dividing circles into pie segments according to the magnitude of the respective fraction items using the same colors as for dot patterns. For instance, 4/7 was drawn by coloring 4/7 of the pie in blue and 3/7 in yellow. The background color used was the same grey as for the other presentation formats. The location of the yellow part varied pseudo-randomly. The diameter of pies ranged from 95 px to 289 px. To ensure that participants cannot select the larger proportion by relying only on the visual area of pie segments, we varied the size of the circles such that in half of the items the larger proportion was also larger in accordance to the visual area of the yellow pie segment, whereas in the other half of the items it was smaller.

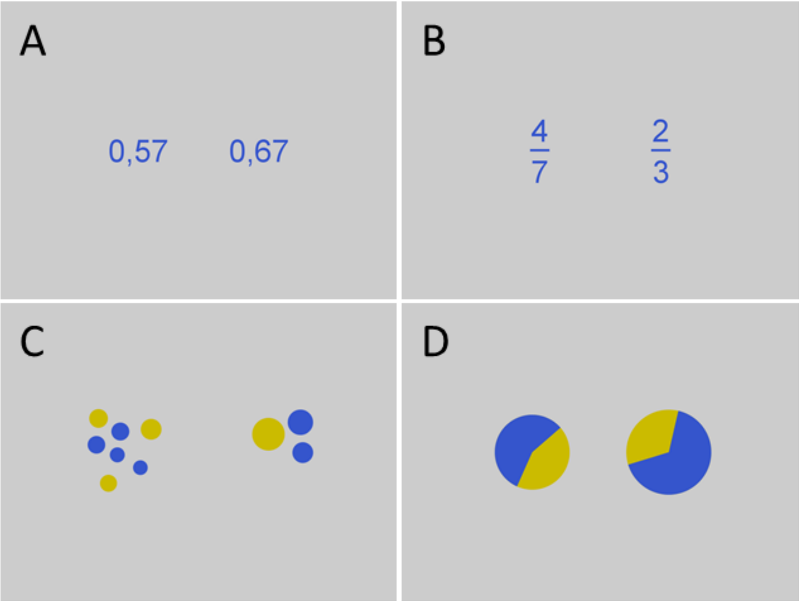

Figure 7.8: Example stimuli (4/7 vs. 2/3) for the four different presentation formats. A depicts decimals, B fractions, C dot patterns, and D pie charts.

fMRI data acquisition

We acquired MRI data using a 3T Siemens Magnetom TrioTim MRI system (Siemens AG, Erlangen, Germany). A high resolution T1-weighted anatomical scan (TR = 2300 s, matrix = 256 × 256, 176 slices, voxel size = 1.0 × 1.0 × 1.0 mm^3; FOV = 256 mm^2, TE = 2.92 ms; flip angle = 8°) was run at the end of the experimental session. All functional measurements covered the whole brain using standard echo-planar-imaging (EPI) sequences (TR = 2,400 ms; TE = 30 ms; flip angle = 80°; FOV = 220 mm^2, 88 × 88 matrix; 42 slices, voxel size = 2.5 × 2.5 × 3.0 mm^3, gap = 10%).

FMRI data was acquired in a single run. We included pauses between blocks each lasting for 6,000 ms and presenting a black screen after each block. Total scanning time was about 20 minutes.

Behavioral data analysis

We analyzed both reaction times and accuracy. Because the distribution of reaction times was strongly skewed to the right, we used the inverse transformation and transformed reaction times into speed with measurement unit 1/sec to approximate normal distribution while conserving statistical power (Ratcliff, 1993). We considered only correctly solved trials in the analysis of speed (84,4% of all trials).

Univariate analyses of variance (ANOVAs) were performed in SPSS (IMB Corp., 2011) to test whether dot patterns, pie charts, fractions, and decimals differed significantly regarding speed and accuracy. Specific comparisons between the four presentation formats were performed using post-hoc Tukey tests ($p < .05$).

fMRI data analysis

Whole-brain analysis

We analyzed fMRI data using SPM12 (http://www.fil.ion.ucl.ac.uk/spm). Images were slice-time corrected, motion corrected, and realigned to each participant's mean image. No participant had to be excluded due to head movements as motion parameters did not exceed 2.5 mm translation in total and a head rotation of 1.5 degree in pitch, roll, and yaw in total. The mean image was co-registered with the whole-brain volume. Then, imaging data was normalized into standard stereotaxic MNI space (Montreal Neurological Institute, McGill University, Montreal, Canada). Images were resampled every 2.5 mm using 4th degree spline interpolation to obtain isovoxel and then smoothed with a 6 mm full-width half-maximum (FWHM) Gaussian kernel to accommodate inter-subject variation in brain anatomy and to increase signal-to-noise ratio in the images. To remove low-frequency noise components the data were high-pass filtered (128s) and corrected for autocorrelation assuming an AR(1) process.

The onsets of the four presentation formats (i.e., fractions, decimals, pie charts, dot patterns) were entered as separate conditions in the GLM. Movement parameters estimated at the realignment stage of preprocessing were included as covariates of no interest. Brain activity was convolved over all experimental trials with the canonical haemodynamic response function (HRF) as implemented in SPM12 and its time and dispersion derivatives.

We conducted a conjunction analysis in order to evaluate the notion of a joint neural substrate of proportion processing (conjunction null; Nichols, Brett, Andersson, Wager, & Poline, 2005). In a second step, we compared activations for the bipartite part-whole relations (i.e., fractions, dot patterns, and pie charts) to decimals to investigate brain activation based on mere part-whole processing.

The SPM Anatomy Toolbox (Eickhoff et al., 2005), available for all published cytoarchitectonic maps (www.fz-juelich.de/ime/spm_anatomy_toolbox), was used for anatomical localization of effects where applicable. In areas not yet implemented, the anatomical automatic labelling tool (AAL) in SPM12 (http://www.cyceron.fr/web/aal anatomical_automatic_labeling.html) was used. For the whole brain analysis, activations were thresholded at a whole-brain family-wise error corrected (FWE) *p*-value of < .05 with a cluster size of *k* = 10 voxels.

Signal change and representational similarity analysis

For percent signal change and representational similarity analyses, we focused on the clusters found in bilateral IPL. Furthermore, we conducted the analyses for both hemispheres separately because it was found that symbolic and non-symbolic formats are processed using both overlapping and distinct neural substrates (Sokolowski et al., 2017). Besides overlapping processing in bilateral IPL, bilateral precuneus, left SPL and right SFG, symbolic number processing (Holloway et al., 2010) and mental calculation (Arsalidou and Taylor, 2011; Dehaene et al., 1999) were especially associated with activation in left IPS. In contrast, parts of right parietal cortex were rather found to be involved in (visuospatial) attentional processes (Arrington et al., 2000; Corbetta et al., 2000; Thiel et al., 2004), processing of non-symbolic numerosities (Holloway et al., 2010; Sokolowski et al., 2017), and magnitude processing (Mock et al., 2018; Mussolin et al., 2013; Piazza et al., 2007).

We further investigated the similarity of activation patterns in jointly activated clusters around the bilateral IPS across presentation formats suggesting similar neural representations. For this, we conducted a representational similarity analysis (RSA). The output of the RSA was a matrix (representational similarity matrix) which reflected pairwise correlations between all stimuli. The RSA was based on β estimates of the voxels within jointly activated clusters in IPL. To obtain the representational similarity matrix, we ran Pearson correlations between the four presentation formats for each participant separately, scaled them into [0, 1] by computing the similarity value sim = (r+1)/2, and then averaged similarity values across participants. The higher the value of similarity (sim), the more similar was the neural representation of the different presentation formats with 1 being most similar. Visualized similarity served to characterize the shared representation (Kriegeskorte et al., 2008).

In course of the RSA, we further conducted an agglomerative hierarchical cluster analysis based on the mean z-standardized β estimates for the four different notation formats. In the hierarchical cluster analysis, we used the Euclidean distance as distance measure and average linkage clustering as linkage criterion with lower distance being more similar.

Appendix

Table A7.1: Activations found for magnitude comparisons with fractions. Activations were thresholded at a whole-brain FWE *p*-value of < .05 with a cluster size of *k* = 10 voxels.

Contrast	Brain region	MNI (x, y, z)			*k*	*t*
Fractions vs. Baseline	LH Inferior parietal lobule	-47	-37	48	1101	12.07
	LH Intraparietal sulcus (hIP3)*	-32	-50	48		11.23
	LH Superior parietal lobule*	-25	-62	45		10.62
	RH Intraparietal sulcus (hIP2)	46	-40	48	1052	10.82
	RH Intraparietal sulcus (hIP3) *	36	-50	48		10.48
	RH Intraparietal sulcus (hIP1) *	28	-55	48		9.15
	LH Precentral Gyrus (Area 44)	-45	6	30	679	11.04
	LH Inferior frontal gyrus (Area 45) *	-45	31	23		7.42
	RH Inferior frontal gyrus (Area 44)	46	6	25	311	10.39
	RH Middle frontal gyrus (Area 45)	48	36	23	225	9.94
	RH Superior frontal gyrus	28	1	53	149	8.30
	LH Middle frontal gyrus	-25	1	55	90	7.65
	LH Inferior frontal gyrus	-47	43	10	53	5.90
	RH Insula	33	26	0	170	10.64
	LH Insula	-30	23	3	127	9.56
	LH Thalamus	-22	-27	-3	60	13.12
	RH Thalamus	23	-27	-3	51	10.55
	RH supplementary area	6	18	48	431	10.72
	RH Lingual gyrus	16	-97	-8	4891	25.15
	RH Calcarine gyrus*	23	-100	-3		24.89
	LH Inferior occipital gyrus*	-22	-95	-10		22.95
	LH Inferior occipital gyrus*	-12	-100	-8		22.21
	LH Middle occipital gyrus*	-15	-92	-8		21.44
	LH Middle occipital gyrus*	-22	-100	3		20.37
	RH Cuneus*	16	-102	8		19.57
	LH Calcarine gyrus*	-5	-90	-5		18.17
	LH Lingual gyrus*	-10	-90	-15		17.67
	RH Calcarine gyrus*	13	-90	3		17.24
	LH Cerebellum (VII)	-32	-67	-50	26	7.23

Abbreviations: *k* = cluster size; LH = left hemisphere; MNI: Montreal Neurological Institute; RH = right hemisphere; *t* = *t*-value. * Minor maximum.

Table A7.2: Activations found for magnitude comparison with decimals. Activations were thresholded at a whole-brain FWE *p*-value of < .05 with a cluster size of *k* = 10 voxels.

Contrast	Brain region	MNI (x, y, z)			*k*	*t*
Decimals	LH Inferior parietal lobule	-45	-32	43	66	6.08
vs.	LH Postcentral Gyrus*	-50	-27	55		5.73
Baseline	RH Postcentral Gyrus	51	-25	48	40	5.74
	LH Thalamus	-22	-17	-3	58	11.73
	RH supplementary motor area	1	6	53	169	7.86
	RH Calcarine gyrus	16	-97	-5	3797	30.74
	LH Middle occipital gyrus*	-15	-92	-8		28.40
	LH Inferior Occipital gyrus*	-12	-100	-8		27.65
	LH Calcarine gyrus*	-17	-100	-5		26.87
	RH Cuneus*	16	-102	8		22.10

Abbreviations: *k* = cluster size; LH = left hemisphere; MNI: Montreal Neurological Institute; RH = right hemisphere; *t* = *t*-value. * Minor maximum.

Table A7.3: Activations found for magnitude comparison with dot patterns. Activations were thresholded at a whole-brain FWE *p*-value of < .05 with a cluster size of *k* = 10 voxels.

Contrast	Brain region	MNI (x, y, z)			*k*	*t*
Dot patterns	RH Calcarine gyrus	16	-97	-5	9332	28.43
vs.	RH Intraparietal sulcus (hIP2)**	46	-35	48	716	12.84
Baseline	RH Intraparietal sulcus (hIP3) **	36	-50	50		12.59
	LH Inferior parietal lobule **	-47	-37	48	480	13.24
	LH Intraparietal sulcus (hIP3) **	-32	-50	48		11.53
	LH Middle occipital gyrus*	-15	-92	-8		26.54
	RH Lingual gyrus*	18	-90	-8		26.16
	RH Superior occipital gyrus*	23	-97	5		25.69
	LH Inferior occipital gyrus*	-12	-100	-8		25.26
	LH Calcarine gyrus*	-17	-100	-5		24.73
	RH Cuneus*	16	-100	10		21.79
	RH Precentral gyrus	43	6	28	772	11.25
	RH Middle frontal gyrus*	43	36	18		10.82
	RH Inferior frontal gyrus (Area 45) *	48	13	30		10.44
	LH Precentral gyrus	-42	1	33	359	9.36
	RH Superior frontal gyrus	28	1	53	326	9.33

	LH Superior frontal gyrus	-25	-2	53	152	8.45
	LH Inferior frontal gyrus	-37	28	20	143	6.91
	LH Middle frontal gyrus	-45	53	0	110	6.18
	RH Middle frontal gyrus	38	58	8	100	5.31
	RH Insula	33	26	0	251	11.03
	RH Putamen*	23	16	0		5.23
	LH Insula	-30	23	3	187	9.81
	LH Putamen	-22	6	3	58	5.60
	RH Thalamus	23	-27	-3	54	10.22
	LH Thalamus	-22	-27	-3	47	11.83
	RH supplementary area	6	18	48	543	11.59
	LH Cerebellum (VIII)	-30	-67	-50	73	8.79
	RH Cerebellar Vermis (9)	1	-55	-35	27	7.44

Abbreviations: *k* = cluster size; LH = left hemisphere; MNI: Montreal Neurological Institute; RH = right hemisphere; *t* = *t*-value. * Minor maximum; ** Secondary peak.

Table A7.4: Activations found for magnitude comparison with pie charts. Activations were thresholded at a whole-brain FWE *p*-value of < .05 with a cluster size of *k* = 10 voxels.

Contrast	Brain region	MNI (x, y, z)			*k*	*t*
Pie charts	RH Postcentral gyrus	48	-25	45	989	10.10
vs.	RH Superior parietal lobule (hIP3)*	33	-45	48		8.07
Baseline	RH Inferior parietal lobule (hIP2)*	41	-40	50		7.85
	RH Inferior parietal lobule (hIP3)*	31	-55	53		7.35
	LH Postcentral gyrus	-42	-35	43	665	9.40
	LH Superior parietal lobule (hIP3)*	-37	-45	58		7.77
	LH Inferior parietal lobule (hIP3)*	-32	-45	48		7.06
	RH Middle frontal gyrus	31	-2	55	103	6.90
	RH Superior frontal gyrus*	28	-5	63		6.31
	RH Inferior frontal gyrus	46	6	25	95	6.85
	LH Precentral gyrus	-50	3	30	66	6.42
	LH Thalamus	-22	-27	-3	74	13.64
	RH Thalamus	23	-27	-3	59	10.54
	LH Putamen	-22	8	3	54	6.01
	RH supplementary area	1	6	53	258	8.76
	RH Calcarine gyrus	16	-97	-5	5439	28.29
	LH Calcarine gyrus*	-12	-92	-8		26.54

LH Inferior occipital gyrus*	-12	-100	-8		25.75
RH Superior occipital gyrus*	23	-97	5		24.94
LH Calcarine gyrus*	-17	-100	-5		24.81

Abbreviations: *k* = cluster size; LH = left hemisphere; MNI: Montreal Neurological Institute; RH = right hemisphere; *t* = *t*-value. * Minor maximum.

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Declarations of interest

None.

Authors' contributions

EK and KM conceived the study. KM, EK, and SH participated in its design. JB and JB performed data collection. JM and SH performed processing and statistical analyses. JM drafted the manuscript; all other authors revised it critically. All authors contributed to the interpretation of the data. All authors read and approved the final manuscript.

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8 Study 3: Negative numbers are not yet automatically associated with space in 6th graders[11]

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Abstract

The metaphor of the mental number line accounts for numerous empirical effects of spatial-numerical associations. In the present study, we aimed at investigating directional spatial-numerical associations reflected by SNARC-like digit-direction and sign-direction congruency effects as well as the sign-digit compatibility effect (Huber et al., 2014) when 6th graders performed magnitude comparisons of multi-symbol numbers (i.e., positive and negative numbers). As spatial-numerical associations were associated with sensori-motor experiences, we used whole-body and finger tapping responses to manipulate the extent of motor responses. We only observed a SNARC-like digit-direction congruency effect, but neither a sign-direction congruency nor a sign-digit compatibility effect. This indicates that 6th graders may already have developed spatial-numerical associations for absolute number magnitude, but not yet for polarity signs. Furthermore, not observing a sign-digit compatibility effect seemed to suggest that 6th graders may not yet process multi-symbol numbers in the same parallel componential way as adults do. We argue that while 6th graders are able to process negative numbers, they are not yet automatically associated with space or integrated in the place-value structure of the Arabic number system like multi-digit numbers are at this age.

8.1 Introduction

A common metaphor to describe the mental representation of number magnitude is the *mental number line* (henceforth MNL). It implies that there is a spatial dimension to the representation of number magnitude in that it is automatically associated with a spatial position on the MNL (Fischer & Shaki, 2014; Nuerk et al., 2015). These spatial-numerical associations (henceforth SNAs) have long been viewed as one big melting pot and have not been further differentiated (e.g., Shaki & Fischer, 2014). Recently, however, a differentiation between SNAs relying on extensions vs. directions was proposed (Cipora, Patro, & Nuerk, 2015; Cipora, Schroeder, Soltanlou, & Nuerk, in press; Patro, Nuerk, Cress, & Haman, 2014).

For extensions, numerical magnitude is associated with spatial extensions, such as numerosity-length matching (de Hevia & Spelke, 2010), extension of abstract rules across different spatial-numerical dimensions (Lourenco & Longo, 2010) or line bisection (de Hevia & Spelke, 2009). For directions, numerical magnitude is associated with a certain direction in space, this means larger numbers are usually associated with *right* in horizontal direction (Dehaene, Bossini, & Giraux, 1993) or *up* in vertical direction (Ito & Hatta, 2004).

In this article, we focus on three specific directional SNAs – the digit-direction congruency (cf. SNARC effect; Dehaene et al., 1993), the sign-direction congruency (i.e., congruent: - = left, + = right, cf. OSSA effect; Pinhas et al., 2014), and the sign-digit compatibility effect – by means of directional horizontal movements (e.g., whole-body or finger tapping) in reaction to multi-symbol numbers (e.g., positive and negative numbers consisting of a polarity sign and a digit, i.e., -5 and +3) in 6th graders.

In the following, we will first give a short overview of recent literature of directional SNAs for symbolic numbers and operation signs before we turn to multi-symbol number processing and the aim of the present study.

Directional SNAs for symbolic numbers

The most prominent effect reflecting directional SNAs for symbolic numbers is the so-called Spatial-Numerical Associations of Response Codes (SNARC) effect. It describes the finding that small numbers are responded to faster with the left and large numbers with the right hand even when number magnitude was irrelevant to the task at hand (e.g., in parity judgment, e.g., Dehaene et al., 1993; see Wood et al., 2008 for a review and meta-analysis). This effect is assumed to originate from a left-to-right oriented MNL resulting in faster responses when response side and position of the respective number on the MNL are congruent (i.e., left – small and right – large; Dehaene et al., 1993; Gibson and Maurer, 2016; Nuerk et al., 2005). This effect was observed using lateral response keys (for an overview, see Fischer and Shaki, 2014), but also directional head (Loetscher, Bockisch, & Brugger, 2008), eye (Fischer, Warlop, Hill, & Fias, 2004; Loetscher, Bockisch, Nicholls, & Brugger, 2010), finger (U. Fischer, Fischer, Huber, Strauß, & Moeller, 2018), or whole-body movements (U. Fischer et al., 2016; U. Fischer, Moeller, Bientzle, Cress, & Nuerk, 2011; Shaki & Fischer, 2014), in adults, but also patients (Zorzi, Bonato, Treccani, Scalambrin, & Marenzi, 2012), participants with limited visual experience (Crollen, Dormal, Seron, Lepore, & Collignon, 2013), or children (Berch, Foley, Hill, & McDonough Ryan, 1999; Gibson & Maurer, 2016; Hoffmann, Hornung, Martin, & Schiltz, 2013; White, Szucs, & Soltész, 2012).

The first study to investigate the SNARC effect for symbolic numbers in children using a parity judgment task concluded that children only showed a significant symbolic SNARC effect from Grade 3 on (mean: 9.2 years; Berch et al., 1999, see also van Galen & Reitsma, 2008; but see De Hevia, Girelli, Addabbo, & Cassia, 2014; de Hevia, Veggiotti, Streri, & Bonn, 2017; Patro & Haman, 2012 for findings of SNARC-like effects for non-symbolic magnitudes already in newborns, infants, and preschoolers). However, White and colleagues (2012) observed a significant symbolic SNARC effect based on parity judgments already in second graders (mean age: 7.5 years; for similar results in a magnitude-relevant task, see also Gibson and Maurer, 2016). Yet, Hoffmann and colleagues (2013) found a SNARC-like effect in an adapted digit color judgment task in which 5.8-year-old children had to indicate the color of a centrally presented number (e.g., red or green) with either their left or right hand. Thus, children implicitly responded faster with their left hand to smaller digits and with their right hand to larger digits.

Interestingly, Chinese children exhibited a symbolic SNARC effect based on the traditional parity judgment task already at an age of 5 years (Yang, Chen, Zhou, Xu, & Dong, 2014). Thus, they already developed automatic directional SNAs for symbolic numbers at this early age which might be due to earlier mathematical instruction in Chinese children and consequently longer experience with symbolic numbers (Yang et al., 2014; Zhou et al., 2007).

In sum, the SNARC effect is argued to reflect a directional spatial representation of number magnitude. During early childhood, SNAs seem to develop through cultural and social experiences such as monitoring adult reading behavior, pretending to read or to write, attentional-directional preferences, and direct spatial-numerical learning (e.g., Göbel, McCrink, Fischer, & Shaki, 2018; Nuerk et al., 2015; Patro, Fischer, Nuerk, & Cress, 2015). With increasing age, SNAs were found to become stronger with children exhibiting robust directional SNAs for symbolic numbers at an age of 7 years (at least in Western children; White et al., 2012) and already earlier in children who received earlier mathematical instruction (Yang et al., 2014).

Older children (*M* = 10;0 years) with an established concept of number magnitude showed a significant SNARC in a magnitude comparison task for both whole-body movement and verbal responses (U. Fischer et al., 2016). However, the authors also investigated the relative numerical congruity effect. Two numbers are congruent when the direction of the answer corresponds to the spatial positioning of a target number on the MNL (e.g., comparison of 2 to 3 when a response to the left is necessary for the smaller number 2). In contrast, two numbers are incongruent when the direction of the answer and the spatial positioning of a target number are distinct (e.g., comparison of 3 to 2 where a response to the right is necessary for the small number 3; for more information, see Fischer et al., 2016). Fischer and colleagues (2016) found stronger activation of SNAs reflected by the relative numerical congruity effect in embodied conditions.

The directional spatial aspects of number magnitude seem associated with children's numerical learning and can, in turn, facilitate numerical understanding (U. Fischer, Link, Cress, Nuerk, & Moeller, 2014; U. Fischer et al., 2011). In particular, responding with whole-body left-right movements on a digital dance mat in a number comparison task positively influenced preschoolers' performance, improved their mental number line representation and other basic numerical competencies such as counting (U. Fischer et al., 2011). On the one hand, this suggests a benefit of spatial-numerical associations for children's basic numerical development. On the other hand, these results also show that embodied experiences of number magnitude through whole-body movements on a dance mat support the development of spatial-numerical associations, and thus, enhance the understanding of number magnitude on the MNL (U. Fischer et al., 2011; for an overview on embodied learning, see Dackermann, Fischer, Nuerk, Cress, & Moeller, 2017).

Thus, for establishing a directional SNA bodily experiences such as whole-body movements can be supportive (Patro et al., 2015). Importantly, it seems that physical actions in form of whole-body movements increase activation of SNAs reflecting the tight link between number magnitude representations and physical space (U. Fischer et al., 2016).

Directional SNAs for operation and polarity signs

Importantly, directional SNAs are not limited to processing numbers. Instead, also the mere presentation of an arithmetic operation sign (i.e., + / -) yields another category of directional SNAs, the so-called operation sign space association (OSSA) effect (Cipora et al., in press; Pinhas, Shaki, & Fischer, 2014). In particular, Pinhas, Shaki, and Fischer (2014) found that adults responded to faster with their left hand when presented with a minus sign and faster with their right hand when presented with a plus sign in an operation sign classification task. Thus, they seemed to shift their attention automatically along the MNL in the direction of the operation indicated by the respective operation sign: to the left when subtracting and to the right when adding (Pinhas et al., 2014).

In line with this notion, Mathieu and colleagues (2017) found that the mere perception of a plus sign elicited more pronounced neural activation in brain areas associated with overt spatial attention shifting (e.g., frontal eye fields, posterior superior parietal lobule) than the perception of a multiplication sign. In contrast to these results for adults, the right hippocampus seemed to contribute to the association between operation signs and space in children (Mathieu et al., 2018). The right hippocampus was reported to be involved in spatial representations and navigation (Burgess, Maguire, & O'Keefe, 2002; Maguire et al., 1998). Importantly, Mathieu and colleagues (2018) observed a grade-related increase of activity in this brain region with children only showing significant activation in response to the plus sign by Grade 7. This mechanism might enable children to construct a representation of arithmetic operations in mental space with increasing age and experience (Mathieu et al., 2018). Furthermore, during development there seems to appear a shift from hippocampal to fronto-parietal activation for operation signs (Mathieu et al., 2017, 2018). However, we are not aware of any study showing the behavioral OSSA effect in children.

Directional SNAs for place-value processing

Recently, place-value processing was also considered in the taxonomy of SNAs (Cipora et al., in press) because processing space (i.e., digit position) and number (i.e., value of the digit) have to be integrated. It is important to note that this also holds true for specific symbols such as polarity signs (e.g., -3 < 3) or the decimal point (e.g., 3.48 < 34.8). Hence, besides the spatial position of a digit also the spatial position of a symbol determines the value of a number. In the present study, we focus on SNAs in processing multi-symbol numbers such as positive and negative numbers. A study by Fischer (2003) suggests that the MNL seems to extend to the left for negative numbers in adults. Yet, it was also found that negative numbers may be processed less automatically compared to positive numbers and, in turn, induce weaker SNAs (Fischer & Rottmann, 2005; Nuerk & Willmes, 2004). This might be because the processing of the polarity sign leads to additional processing loads comparable to an additional digit in a multi-digit number (Huber, Cornelsen, Moeller, & Nuerk, 2014).

In fact, it was shown that adults process multi-symbol numbers in the same decomposed fashion as multi-digit numbers (Huber, Cornelsen, Moeller, & Nuerk, 2014; see Huber, Bahnmueller, Klein, & Moeller, 2015 for evidence from computational modelling). In multi-digit numbers, individual digits are processed separately but in parallel as indicated by the unit-decade compatibility effect in two-digit number comparison (e.g., compatible trials: 68 vs. 35, 6 > 3 and 8 > 5; incompatible trials: 18 vs. 35, 1 < 3, but 8 > 5; see Moeller et al., 2009; Nuerk et al., 2001). Although comparing decade-digits would be sufficient to choose the larger number, the comparison of unit-digits interferes, and in turn, leads to slower responses. Interestingly, the unit-decade compatibility effect was found to increase with increasing age and experience reflecting more parallel and automated processing (Mann, Moeller, Pixner, Kaufmann, & Nuerk, 2011). Interestingly, two-digit numbers were observed to be processed in parallel in children from 1st grade on (Mann et al., 2011; Pixner et al., 2011). However, parallel processing for more complex three-digit numbers was not observed before 3rd grade (Mann, Moeller, Pixner, Kaufmann, & Nuerk, 2012). Thus, parallel componential processing of individual digits seems to depend on age and experience with the respective numerical concept.

For multi-symbol numbers, it is assumed that the polarity sign is processed comparable to an individual digit in a multi-digit number as similar interference was observed (Huber et al., 2014; but see Ganor-stern et al., 2010; Shaki and Petrusic, 2005; Varma and Schwartz, 2011 for alternative explanations). To evaluate processing of multi-symbol numbers in adults, Huber and colleagues (2014) used a magnitude comparison task with positive and negative two-digit numbers. They found a sign-decade compatibility effect with incompatible trials (-97 vs. +53 in which the larger decade digit has the smaller, i.e., negative polarity sign) leading to slower responses compared to compatible trials (e.g., -53 vs. +97 in which the number with the larger decade digit has the larger, i.e., positive polarity sign). Slower responses found for incompatible trials were explained by interference of the opposing biases resulting from separate comparisons of polarity signs and decade-digits, respectively. This effect provides evidence for parallel componential processing of multi-symbol numbers in adults comparable to the processing of multi-digit numbers (Huber et al., 2014). However, this is the case for adults who are familiar with negative numbers and have an established concept of negative number magnitude. As to our knowledge, there is no study so far investigating multi-symbol number processing in children who were just introduced to negative numbers in school.

Therefore, we also investigated a sign-digit compatibility effect (e.g., compatible: combination of a small number and -, i.e., -2; combination of a large number and +, i.e., +8) in 6th graders evaluating how children process multi-symbol numbers who just learned about negative numbers.

The present study

As described above children seem to gradually develop directional SNAs for symbolic numbers with increasing age and experience showing a robust SNARC effect for symbolic numbers at about the age of 7 years (Gibson & Maurer, 2016; White et al., 2012, see Patro & Haman, 2012; de Hevia et al., 2014, 2017 for earlier findings of non-symbolic SNARC). As children get older their number range extends to negative numbers, which require processing both symbolic numbers and polarity signs. From this, the question arises whether their MNL, and thus their spatial representation of numbers, also extends to the left for negative numbers, and whether children as a consequence also develop directional SNAs for negative numbers.

To pursue this issue, we tested 6th graders who were just introduced to the concept of negative numbers in school on number magnitude comparison with multi-symbol single-digit numbers involving positive and negative numbers (e.g., +4 vs. -7). In particular, according to the mathematics curriculum of Baden-Wuerttemberg, Germany, children are introduced to negative numbers in mathematics instruction at the beginning of 6th grade. This was confirmed by the teachers of the participating classes. Data collection for the current study took place at about the middle of sixth grade and thus, about half a year after children were introduced to negative numbers. We chose this time point on purpose because children had six months to get familiar with the concept of and operate with negative numbers, but were not yet highly experienced with it. Therefore, this seemed as a good time point for evaluating how solid the concept of negative numbers already is. Each child performed the comparison task in a condition with whole-body movements on a digital dance mat and in finger tapping condition on a tablet PC to investigate whether they already developed a spatial-numerical representation of negative numbers. In particular, we included a whole-body response condition because there is evidence suggesting that whole-body response movements should activate spatial-numerical representations more strongly (Fischer et al., 2016). Thus, effects reflecting respective SNAs might be captured elevated using whole-body responses as compared to finger tapping responses if at all possible to obtain them in the latter condition.

Importantly, using a number comparison task with multi-symbol numbers enabled us to investigate three different SNAs:

1. A digit-direction congruency effect: The standard SNARC effects suggests that digits are responded to faster with left when small and faster with the right when large. Importantly, this was also observed for the case of negative numbers, when only negative numbers are presented: -9 was responded to faster with the right and -1 faster with the left hand (Nuerk et al., 2004). This indicates that this spatial association is bound to the absolute number magnitude.
2. A sign-direction congruency effect: As Pinhas and colleagues (2014) showed polarity signs are systematically associated with a specific direction in space (i.e., – = left, + = right).

3. A sign-digit compatibility effect (compatible: combination of a small number and -; combination of a large number and +). This sign-digit compatibility effect was demonstrated by Huber and colleagues (2014) before, but has never been tested in children.

By using these effects to reflect SNAs, we aimed at evaluating the strength of SNAs induced by multi-symbol numbers in children who just learned about negative numbers.

We expected stronger congruency effects for the embodied condition as physical movements were shown to increase activation of SNAs (U. Fischer et al., 2016, 2018). Furthermore, it was shown that children build a spatial representation for symbolic numbers (White et al., 2012; Gibson et al., 2016) and arithmetic operations (Mathieu et al., 2018) with increasing age and experience. Thus, we expected to observe significant digit-direction and sign-direction congruency effects as children by the age of 12 years should already have developed SNAs for symbolic numbers and arithmetic operation or polarity signs.

Additionally, we investigated whether componential parallel multi-digit number processing observed in children from 1st grade on (Mann et al., 2011; Mann et al., 2012) also generalizes to parallel decomposed processing of multi-symbol numbers in 6th graders (Huber et al., 2014). As experience with a specific numerical concept seems to determine the way of processing (i.e., sequential or parallel; Mann et al., 2012), we expected rather sequential processing of multi-symbol numbers in 6th graders who just learned about this numerical concept.

8.2 Method and Materials

Participants

Forty-three German sixth graders (20 girls and 23 boys) aged 11-12 years (M = 11.93; SD = 0.38) participated in the study after the study was approved by local school authorities and written informed consent of their parents was obtained. All children attended the same public high school. One child was excluded from data analysis due to technical problems during the experiment. None of the children exhibited obvious attentional difficulties or signs of neurologic diseases. All children participated in both the whole-body condition on the dance mat and the finger tapping condition on a tablet PC. Half of the children started with either one of the conditions. They were tested in a separate room in their school during regular school hours.

Task and procedure

Children performed magnitude comparison tasks with both positive and negative numbers in a whole-body and a finger tapping condition. Children had to indicate whether the upper number in a box is larger/smaller than a lower number. In both conditions, they performed the same task with identical stimuli. The conditions only differed regarding presentation and response format. In the whole-body condition, children performed the magnitude comparison task on a digital dance mat for whole-body responses while the to-be-compared numbers were projected onto the wall in front of them (see Figure 1A). The fields of the dance mat were arranged in a 3 x 3 layout of which only the middle row and the middle field in the front was used. Either the field to the left or the right of the central field had to be stepped on with both feet to evoke a response (i.e., a step to the left for a "smaller" response and a step to the right for a "larger" response). Afterwards, children were asked to step back to the central field. To see the next item, children then had to touch the middle front field with one foot. The next item was displayed with a delay of 500 ms. In the finger tapping condition, children performed the magnitude comparison task on a tablet PC (see Figure 1B). In the lower third of the tablet PC, a response box was presented. Children responded by touching the left or the right response box with either their left of right index finger.

The to-be-compared numbers appeared simultaneously and remained visible until participants responded either by making a step to one side on the dance mat or by touching on one side of the response box on the tablet PC. No feedback was given as to the correctness of the response. There was a short break after half of the items.

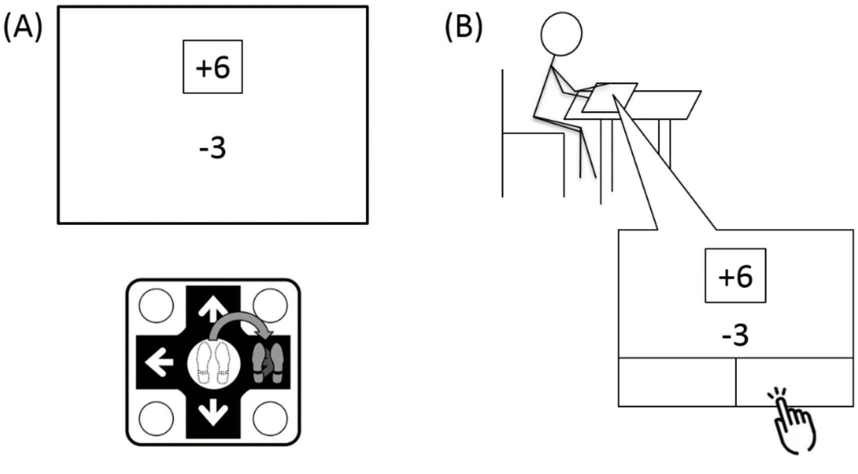

Figure 8.1: Procedure in (A) the whole-body condition on the digital dance mat with the task being projected onto the wall and (B) the finger tapping condition on a tablet PC.

Children were asked to perform the magnitude comparison task twice in each condition. In one run on both the dance mat and the tablet PC, children had to indicate that the upper number in a box is larger/smaller than a lower number by making a step to the right/left on the dance mat or tapping on the right/left response field on the tablet, respectively. In a second run, response assignments were switched. Order of runs was pseudo-randomized.

Stimuli and Design

Identical stimulus sets were used for both conditions consisting of 24 homogeneous positive (e.g. +2 vs. +8), 24 homogeneous negative (e.g., -3 vs. -5), and 24 heterogeneous (e.g., -4 vs. +6) single-digit number pairs that were shown twice. Thus, in sum 144 number pairs were presented. Half of the heterogeneous number pairs (i.e., 12 number pairs presented twice resulting in 24 pairs in total) were sign-digit compatible (e.g., +6 vs. -3 with + > - and 6 > 3). The other half was sign-digit incompatible (e.g., +2 vs. -7 with + > - but 2 < 7). In the heterogeneous pairs, numbers with the same digits (e.g., -4 vs. +4) were excluded. Absolute distance between numbers ranged from 1 to 6.

All number pairs were presented in Arabic notation using 100-point plain Courier New font in black against white background. The polarity sign was shown for positive and negative number pairs. Item order was randomized for each participant individually. The upper and lower number was larger in 50% of the trials, respectively.

Analysis

We analyzed both reaction times (RT) and error rates. Only correct responses were considered for RT analyses. In sum, this resulted in a loss of 9.75% of the data for RT analyses.

Sign-digit compatibility and sign-direction congruency effects can only be analyzed for heterogeneous number pairs. In contrast, for digit-direction congruency effects all number pairs can be analyzed. Therefore, we conducted two separate analysis of variance (ANOVA) for digit-direction congruency on the one hand and sign-digit compatibility as well as sign-direction congruency on the other hand.

Thus, for heterogeneous number pairs we conducted a 2 x 2 x 2 repeated-measures ANOVA with sign-digit compatibility (compatible vs. incompatible), sign-direction congruency (congruent vs. incongruent), and medium (whole-body vs. finger tapping) as factors for RT and error rates, respectively.

For the digit-direction congruency effect, all number pairs (i.e., same signs: ++ and --; mixed signs: +- and -+) were used for the analysis. It is important to note that from the logic of the digit-direction congruency effect in an experiment using positive and negative numbers same sign number pairs in the congruent condition comprise only ++ number pairs (e.g., +5 vs. +7) whereas the same number pairs in the incongruent condition were composed of - - number pairs only (e.g., -3 vs. -6). For example, when participants had to evaluate whether -5 is larger or smaller than -8, they would answer with a step to the right side because -5 is larger than -8. However, the polarity signs are not considered specifically for the digit-direction congruency effect. Considering only the digits, not the polarity signs, the answer would be left because 5 is smaller than 9. Thus, incongruency follows from the direction of participants' response in combination with the polarity signs that, however, are not considered specifically for the analysis of the digit-direction congruency effect. Thus, we conducted a 2 x 2 x 2 repeated-measures ANOVA with digit-direction congruency (congruent vs. incongruent), medium (whole-body vs. finger tapping) and polarity (same signs vs. mixed signs) as factors for RT and error rates, respectively. To allow for a better grasp of the data we also report effect sizes η_G^2 and their 90 % confidence intervals (CI) (Steiger, 2004).

8.3 Results

As sign-digit compatibility and sign-direction congruency can only be analyzed for heterogeneous sign number pairs whereas digit-direction congruency is evaluated for all number pairs, descriptive statistics for the different effects are given in two separate tables.

Table 8.1. Means and standard error of RT (in milliseconds) and error rates (in %) for sign-digit compatibility and the sign-direction congruency. In parenthesis 1 standard error of the mean (SEM) is indicated.

Measure	Sign-digit	Sign-direction	Whole-body	Finger tapping
			M	*M*
RT	Compatible	Congruent	2631 (128)	2156 (136)
		Incongruent	2624 (158)	2130 (145)
	Incompatible	Congruent	2646 (155)	2235 (120)
		Incongruent	2547 (137)	2238 (166)
Error rates	Compatible	Congruent	7.64 (2.57)	5.66 (1.70)
		Incongruent	9.72 (3.27)	8.83 (3.24)
	Incompatible	Congruent	7.74 (2.86)	5.75 (1.89)
		Incongruent	8.73 (3.09)	8.14 (3.06)

Table 8.2. Means and standard errors of RT (in milliseconds) and error rates (in %) for digit-direction congruency further split up in same and mixed sign number pairs for analysis. 1 SEM is given in parenthesis.

Measure	Digit-direction	Polarity	Whole-body	Finger tapping
			M	*M*
RT	Congruent	Same signs	2551 (127)	2039 (96)
		Mixed signs	2640 (130)	2129 (118)
	Incongruent	Same signs	3032 (160)	2577 (102)
		Mixed signs	2594 (136)	2217 (111)
Error rates	Congruent	Same signs	7.14 (2.20)	8.71 (1.62)
		Mixed signs	8.68 (2.88)	7.24 (2.03)

Incongruent	Same signs	11.71 (3.09)	15.38 (2.34)
	Mixed signs	8.23 (2.91)	6.94 (1.98)

RT results

<u>Sign-digit compatibility and sign-direction congruency</u>

RT. The ANOVA revealed a significant main effect of medium ($F(1, 38) = 24.14$, $p < .001$, $\eta_G^2 = .39$; 90% CI = .18; .53) indicating that children answered faster on the tablet PC compared to the whole-body response on the dance mat ($M = 2.14$ s vs. $M = 2.64$ s). This, however, may not be surprising because finger tapping is generally faster than moving the whole body to a specific side in space. The main effects for sign-digit compatibility ($F (1, 38) = 2.41$, $p = .129$, $\eta_G^2 = .06$; 90% CI = .00; .21) and sign-direction congruency ($F < 1$) were not significant. The results are depicted in Figure 8.2A.

These results were further substantiated by Bayesian analyses. Using the method proposed by Masson (2011), graded evidence for the null hypothesis (given the obtained data) can be calculated (see Masson, 2011, for a detailed description of the method).

With respect to the main effect for sign-digit compatibility, Bayesian analysis revealed that the posterior probability of the null hypotheses (i.e., no difference between compatible and incompatible number pairs) was 0.67, which reflects weak evidence for the null hypothesis according to Masson (2011).

Bayesian analysis for the main effect for sign-direction congruency revealed a probability of 0.85 for the null hypotheses (i.e., no difference between congruent and incongruent responses) which – according to Masson (2011) – represents positive evidence for the null hypothesis.

Error rates. The ANOVA revealed no significant main effect for medium ($F < 1$), sign-digit compatibility ($F (1, 41) = 1.28$, $p = .265$, $\eta_G^2 = .03$; 90% CI = .00; .15), or sign-direction congruency ($F (1, 41) = 1.61$, $p = .212$, $\eta_G^2 = .04$; 90% CI = .00; .17). The results are depicted in Figure 8.2B.

Again, we substantiated these results by means of Bayesian analyses. With respect to the main effect for medium, sign-digit compatibility, and sign-direction congruency, the Bayesian analyses revealed that the probabilities of the null hypotheses (i.e., no difference between whole-body and finger tapping responses, no difference between compatible and incompatible number pairs, and no difference between congruent and incongruent responses, respectively) were 0.84, 0.78, and 0.75, respectively, providing positive evidence for the null hypothesis (Masson, 2011).

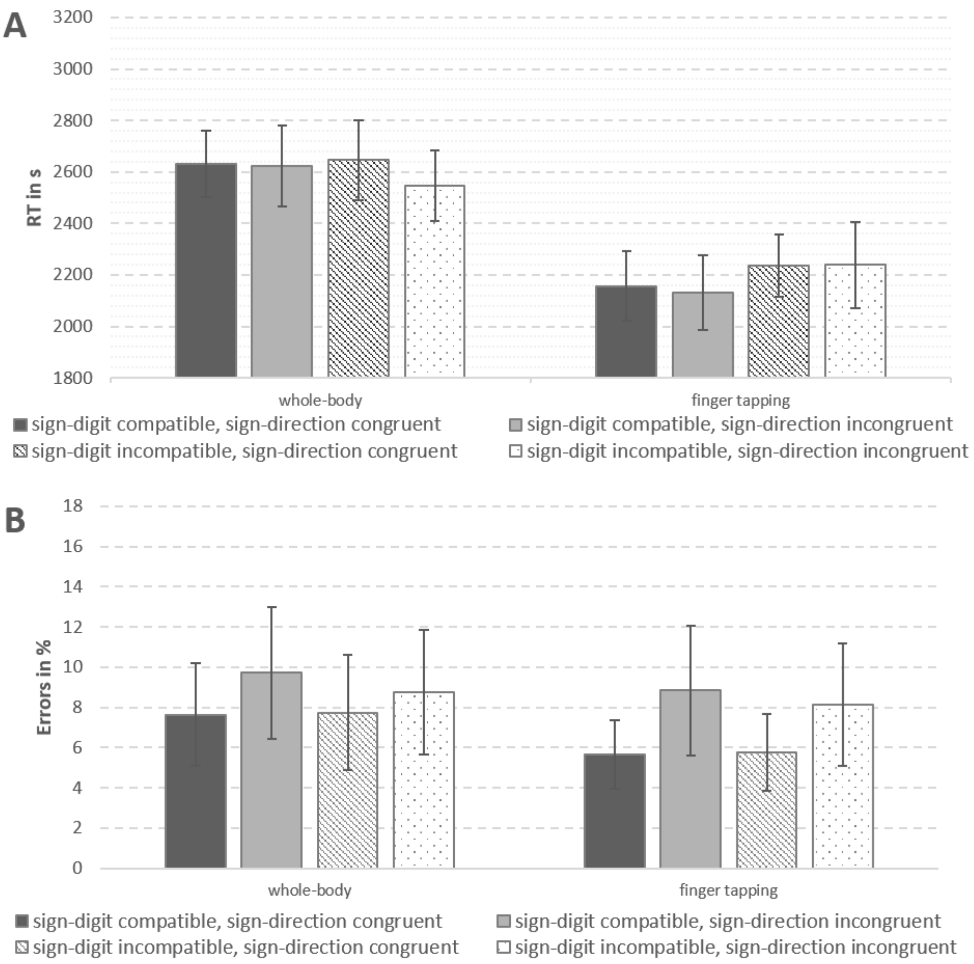

Figure 8.2: Panel A reflects mean reaction times in milliseconds for sign-digit compatibility and sign-direction congruency of whole-body and finger tapping responses further separated by sign-digit compatibility and sign-direction congruency.

Panel B depicts mean error rates in percent for sign-digit compatibility and sign-direction congruency of whole-body and finger tapping responses further separated by sign-digit compatibility and sign-direction congruency. Error bars depict 1 SEM.

Digit-direction congruency

RT. For all number pairs, the ANOVA revealed a significant main effect of medium (*F* (1, 41) = 23.68, $p < .001$, $\eta^2_G = .37$; 90% CI = .17; .51) indicating that responses on the dance mat were again significantly slower than finger tapping on the tablet because they required whole-body movements. Furthermore, the significant main effect of congruency (*F* (1, 41) = 50.54, $p < .001$, $\eta^2_G = .55$; 90% CI = .37; .66) reflected that children were faster in congruent compared to incongruent trials. The significant main effect of polarity (*F* (1, 41) = 13.65, $p = .001$, $\eta^2_G = .25$; 90% CI = .08; .41) further indicated that mixed sign number pairs were responded to faster compared to the same sign number pairs. Furthermore, the interaction between congruency and polarity was significant (*F* (1, 41) = 43.87, $p < .001$, $\eta^2_G = .52$; 90% CI = .32; .63) indicating that the digit-direction congruency effect was larger for same sign number pairs than for mixed sign number pairs. Post hoc pairwise comparisons revealed that the difference between congruent and incongruent responses was significant in the same sign condition (*t*(41) = -9.17, *p* < .001) with congruent responses being faster than incongruent responses in same sign pairs, but not in the mixed sign condition (*t*(41) = -.43, *p* = .667).

Additionally, the difference between same sign and mixed sign number pairs was significant in the incongruent condition (*t*(41) = 6.67, *p* < .001) with mixed sign number pairs being responded to faster than same sign pairs in the incongruent condition, but not in the congruent condition (*t*(41) = -1.70, *p* = .096). The results are depicted in Figure 8.3A.

Error rates. The main effect of congruency reached significance (*F* (1, 41) = 10.33, *p* = .003, η_G^2 = .20; 90% CI = .05; .36) indicating that children responded more accurately in congruent compared to incongruent tasks. Furthermore, the ANOVA revealed a significant main effect for polarity (*F* (1, 41) = 8.28, *p* = .006, η_G^2 = .17; 90% CI = .03; .33) which indicated that mixed sign number pairs were responded to more accurately than same sign number pairs. The interaction between medium and polarity reached significance (*F* (1, 41) = 14.40, *p* < .001, η_G^2 = .26; 90% CI = .09; .42) reflecting that performance differences between same and mixed sign number pairs were more pronounced on the finger tapping on the tablet compared to the whole-body response on the dance mat.

Post hoc tests revealed that the difference between same sign and mixed sign number pairs was only significant in the finger tapping condition with more errors in same sign number pairs than in mixed sign number pairs (*t*(41) = 4.77, *p* < .001; all other pairs *p* > .11).

Moreover, the significant interaction between congruency and polarity (F (1, 41) = 12.65, p = 001, η_G^2 = .24; 90% CI = .07; .40) indicated the same pattern as also found for RT reflecting that the digit-direction congruency effect was larger for same sign number pairs than for mixed sign number pairs.

Post-hoc pairwise comparisons revealed that congruent and incongruent number pairs differed significantly in the same sign condition (t(41) = -3.46, p = .001) with congruent responses being more accurate than incongruent responses (see Table 8.2). Furthermore, the difference between same sign and mixed sign number pairs in the incongruent condition was significant (t(41) = 4.59, p < .001) with mixed sign number pairs being responded to more accurately than same sign pairs. Thus, for the interaction between congruency and polarity the very same pattern of results was observed for RT and error rates. The results for error rates are depicted in Figure 8.3B.

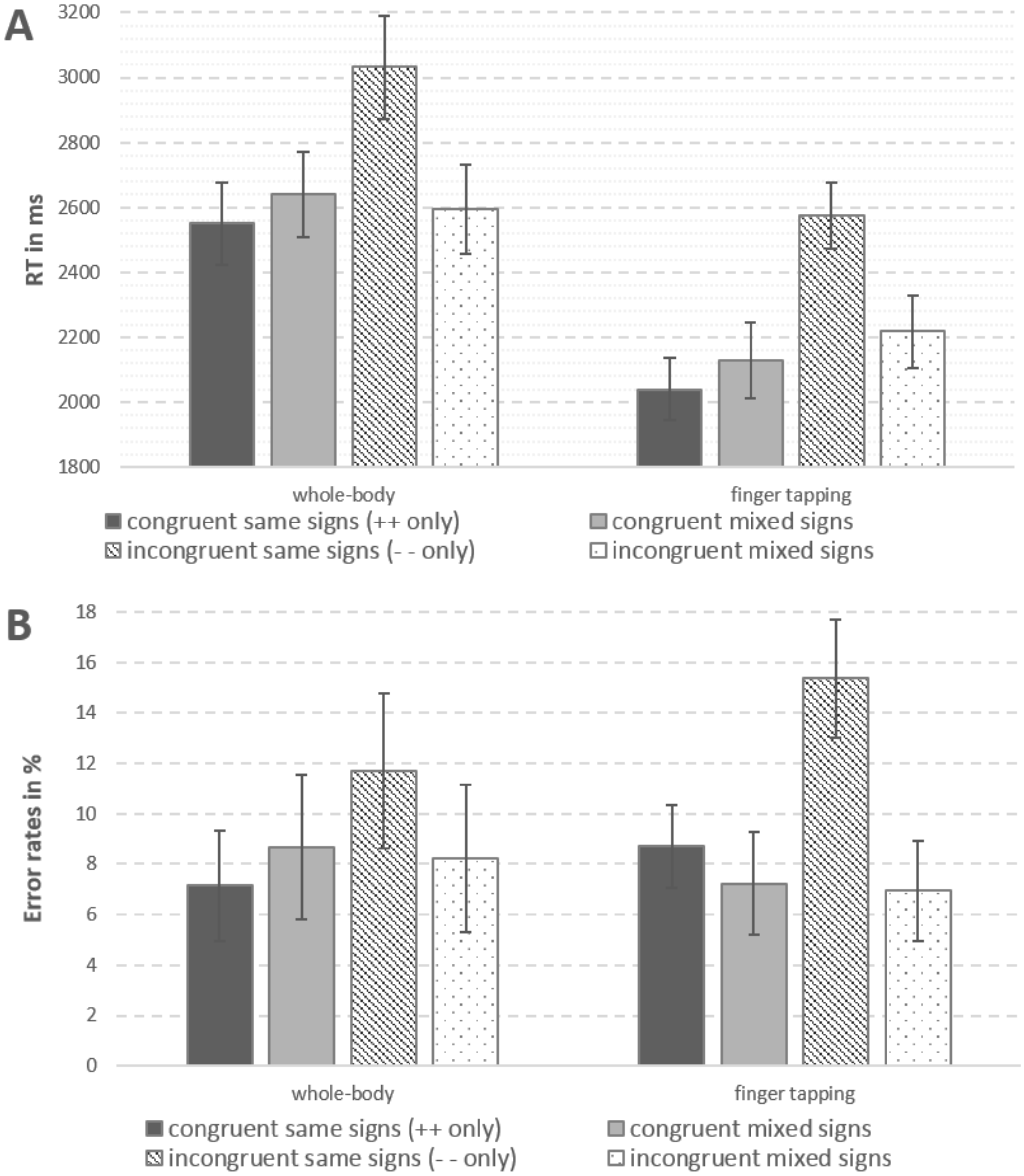

Figure 8.3: Mean reaction times and error rates for digit-direction congruency. A Mean reaction times in milliseconds of whole-body and finger tapping responses further separated for digit-direction congruency and polarity. Error bars reflect 1 SEM.
B Mean error rates in percent of whole-body and finger tapping responses further separated for digit-direction congruency and polarity. Error bars depict 1 SEM.

8.4 Discussion

In the present study, we aimed at evaluating three specific directional SNAs (i.e., digit-direction, sign-direction congruency effect, and sign-digit compatibility effect) in a whole-body movement and a finger tapping condition induced by multi-symbol numbers in children who just learned about negative numbers. Furthermore, using multi-symbol numbers enabled us to investigate how these numbers consisting of a polarity sign and a digit were processed by children. In the following, we will first recapitulate the most important results before discussing them in turn.

RT data showed that finger tapping responses on the tablet PC were significantly faster compared to whole-body responses on the dance mat. This, however, comes as no surprise as it is generally faster to move only a hand or a finger than moving the whole body to a specific side in space.

Yet, more interestingly, we observed a digit-direction congruency effect which is equivalent to a SNARC-like effect for both RT and error rates. Children responded to faster and more accurate with a leftward movement to small and a rightward movement to larger absolute number magnitudes. Thus, 6th graders seemed to associate small (absolute) number magnitudes with the left side of space and large (absolute) number magnitudes with the right side of space.

However, we did not observe a sign-direction congruency effect (cf. OSSA effect; Pinhas et al., 2014) neither for RT nor for error rates as substantiated by Bayesian analysis. This may indicate that 6th graders do not (yet) associate polarity signs with a specific side of physical space.

Additionally, we did not observe a sign-digit compatibility effect for RT or error rates – again substantiated by Bayesian analysis – indicating that 6th graders may not (yet) process polarity signs and digits in a parallel componential manner like adults do (Huber et al., 2014). These results will be discussed in the following.

SNAs induced by number magnitude, but not polarity signs

A significant SNARC-like effect, this means the digit-direction congruency effect in RT and error rates, was observed for 6th graders. In line with previous research, this indicates that absolute number magnitude was associated with a specific side in space: Small numbers are associated with the left, whereas large numbers are associated with the right side in space (Dehaene et al., 1993; Ninaus et al., 2017; van Galen & Reitsma, 2008; White et al., 2012).

However, we did neither find a sign-direction congruency effect in RT nor in error rates as further substantiated by Bayesian analysis. This might indicate that 6th graders do not yet associate polarity signs with a specific side in space. Rather, this suggests that children undergo a development until they associate the plus sign with the right and the minus sign with the left side in space. This is in line with Mathieu and colleagues (2018) who only found significant activation in brain regions associated with spatial processing as a response to a plus sign from grade 7 on. Ninaus and colleagues (2017) showed that directional SNAs (in their case the SNARC effect) strengthened with increasing age and experience reflecting a development towards an automatic association between number magnitude and physical space. This might also be the case for a directional SNA for polarity signs. Thus, although 6th graders already acquired conceptual knowledge about multi-symbol (i.e., negative) numbers as indicated by their ability to solve the task, the current results also suggest that they did not yet automatically associate polarity signs with space.

Importantly, there is an interesting distinction between polarity signs and arithmetic operation (signs), which is worth mentioning here. Children are familiar with plus and minus signs indicating the corresponding arithmetic operations of addition and subtraction since 1st grade. Additionally, children were observed to show an operational momentum effect (i.e., overestimation of addition and underestimation of subtraction outcomes) from the age of 9-months on in non-symbolic arithmetical tasks (e.g., McCrink & Wynn, 2009) and with increasing age and math proficiency also for symbolic arithmetic (e.g., Pinhas & Fischer, 2008). Thus, plus and minus signs can induce spatial numerical associations in terms of the operational momentum effect, whereas they did not (yet) seem to do so when used as polarity signs in the context of multi-symbol numbers in our sample of 6th graders. A potential explanation for this might refer to theories of embodied cognition which assumes abstract representations such as number magnitude to be (at least partially) rooted in bodily and physically perceivable interactions and experiences with the environment (e.g., Domahs, Moeller, Huber, Willmes, & Nuerk, 2010; Moeller et al., 2012). As long as children operate within natural numbers, there is an embodied representation of addition and subtraction: Peter can have five marbles and get another two (= addition) or give away three of them (= subtraction). The operation can be perceived physically (e.g., using one's fingers) even without knowing that an arithmetic operation is going on. Thus, arithmetic operations like addition and subtraction can be grounded and bound to physical experiences (Domahs et al., 2010; Moeller et al., 2012). However, there is no embodied or physically perceivable experience for negative numbers. Text problems cannot start with Peter having -5 marbles or having two cookies and giving six away. As such, the concept of negative numbers may not be grounded in nature but reflects an abstract mathematical concept. Thus, for natural numbers arithmetic operation (signs) may be grounded and bound to experience, whereas this is not possible for negative numbers per se and, in turn, for polarity signs. This might also be the reason why spatial associations develop earlier for arithmetic operations such as addition and subtraction compared to negative numbers and polarity signs, in particular (Huber et al., 2014).

This assumption is further substantiated by our results on the SNARC-like digit-direction congruency effect. Both RT and error rates indicate that 6th graders needed longer and made more errors when they had to compare two negative numbers (i.e., incongruent same sign condition). It seemed as if they followed a two-step strategy: First, they might follow a mirroring strategy internally transforming negative digits to positive ones before actually comparing magnitudes in a second step (Krajcsi & Igács, 2010). Such a procedure might lead to longer RTs and more errors, and furthermore reflects a non-automatic processing of negative numbers in 6th graders. Interestingly, similar brain activation for positive and negative numbers were found in 7th graders but not yet in 5th graders (Gullick & Wolford, 2014). These differences in brain activation might be due to the fact that 5th graders not yet automatically associate negative numbers with space as 7th graders did in the study by Gullick and Wolford (2014).

Our behavioral data support this argument showing that negative numbers are processed and represented differently from positive numbers in children who just learned about this concept.

Yet, the current data also indicated that 6th graders nevertheless consider the polarity sign during their decision process. For the digit-direction congruency effect, we found that there is no difference between congruent number pairs (e.g., -3 vs. +8) and incongruent mixed sign pairs (e.g., -8 vs. +3) neither in RT nor in error rates. This indicates that they may have based their decision primarily on the differing polarity sign in terms of using a sign shortcut strategy. When children would have relied on processing (absolute) number magnitude only, they should also have followed a mirroring strategy, which should have led to differing results. However, relying on polarity signs exclusively is already sufficient to answer correctly in heterogeneous number pairs and thus no processing of digit magnitude is necessary. Furthermore, children made, in fact, fewer errors in this condition compared to incongruent same sign number pairs. Thus, the current results indicate that 6th graders at least partly used a sign shortcut strategy for decision making (Krajcsi & Igács, 2010). Additionally, same sign number pairs were answered less accurate than mixed sign number pairs in the finger tapping condition. This effect was mainly driven by incongruent same sign number pairs (e.g., -2 vs. -6), in which children had to apply a mirroring strategy to solve the task correctly (Krajcsi & Igács, 2010). Although speculative, more errors in the finger tapping condition might result from shorter reaction times in this condition. In the finger tapping condition children answered significantly faster than in the whole-body condition. In turn, decisions might have been reconsidered and corrected if necessary in the whole-body movement because longer movement times may have allowed for doing so. In contrast, children responded fast and fluently in the finger tapping condition and may not have been able to reconsider a decision while on the way and thus commit an error. This account is, however, speculative and requires further research.

The present results suggest that when processing multi-symbol numbers, the magnitude of the digit may not necessarily be activated automatically to create interference in the case of mixed sign pairs. This is because the magnitude of the digit would interfere only when the two components of a multi-symbol number are processed in parallel. However, as only a significant sign-digit compatibility effect would indicate parallel processing of the polarity sign and the corresponding digit, the observed null effect for sign-digit compatibility further supports this assumption. Thus, the integration of polarity sign and digit seems to be less automatic in 6th graders than the integration of digits into the place-value system in multi-digit numbers in children (Mann et al., 2011, 2012) or the integration of polarity sign and digit in adults (Huber et al., 2014).

Importantly, these results suggest differential development of automatic associations with space for different numerical concepts in the way that SNAs for different numerical concepts develop at different time points depending on experience with this specific concept (Mann et al., 2011, 2012; Nuerk, Kaufmann, Zoppoth, & Willmes, 2004).

In sum, in 6th graders, (absolute) number magnitude seems to be the primary determinate of SNAs rather than polarity signs. It is important to note, however, that we did not present polarity signs exclusively in the present study. Thus, magnitude information of symbolic numbers might always have had an influence on processing the polarity sign and vice versa. This might also be one reason why we did not observe a sign-direction congruency effect: Number magnitude might have elicited stronger spatial associations than the polarity sign, and hence, might overrule an existing, but weaker association of polarity signs and space. As polarity sign and digit may, however, not yet be integrated, and thus, not processed in parallel at that age, interferences of digit magnitude may not be observed in mixed number pairs. To disentangle this issue, further research is needed.

Nevertheless, our results seem to indicate that the association between number magnitude and physical space might be stronger or at least developed earlier in life than the association of polarity signs and space (i.e. the non-significant sign-direction congruency effect) at this age. This might be the case because 6th graders are more experienced with (absolute) number magnitude than they are with multi-symbol numbers or polarity signs. The association of number magnitude and space was found to strengthen with time, experience, and education (Kucian, Plangger, O'Gorman, & Von Aster, 2013; Ninaus et al., 2017; Nuerk et al., 2015). In contrast, the concept of negative numbers is relatively new to 6th graders.

This is also in line with theoretical accounts on embodied numerical representations (Fischer, 2012; Fischer & Brugger, 2011). These suggest that sensori-motor experiences shape human cognition and are the foundation of higher cognitive concepts, also including numbers, in every individual (Fischer, 2012). Together with cultural and social mechanisms like reading and writing behavior or monitoring adult reading behavior in younger children, attentional-directional preferences (temporal ordering or even applications for electronic devices), or direct spatial-numerical learning in picture books, these embodied representations support the development of SNAs (Nuerk et al., 2015). Thus, these influences reflect culturally determined sensori-motor experiences that strengthen with increasing age and experience (Ninaus et al., 2017). As 6th graders are more familiar with number magnitude than with polarity signs due to longer experiences, it seems plausible that the SNA for number magnitude were stronger than for polarity signs at that age.

Taken together, despite current limitations, the present study provides evidence suggesting directional SNAs for number magnitude, but not yet for polarity signs in 6th graders who just learned about negative numbers.

Processing of multi-symbol numbers in children

As the value of a digit is defined inherently by its spatial position in the digit-string of multi-digit numbers, they yield another category of directional SNAs. To investigate processing characteristics of multi-digit or multi-symbol numbers, the compatibility effect is often used (Huber et al., 2014; Moeller et al., 2009; Nuerk & Willmes, 2005). By means of the compatibility effect, it was shown that in multi-symbol numbers in which the comparison of the polarity signs is sufficient for decision making digit magnitude nevertheless interfered (e.g., -8 vs. +3; - < +, but 8 > 3, e.g. Huber et al., 2014). This effect suggests parallel, but componential processing of multi-symbol numbers in adult participants. Thus, adults who are familiar with multi-symbol numbers process the constituting components (e.g., polarity signs and digits) in parallel, but not as an integrated entity.

However, we did not find a sign-digit compatibility effect neither in RT nor in error rates of 6th graders in the current study as further substantiated by Bayesian analysis. Thus, although 6th graders already learned about negative numbers and had to perform calculations on them in school, they did not seem to process the polarity sign and the digit of a multi-symbol number in a parallel componential way as adults do. Instead, it seems more likely that children use a more sequential strategy to access magnitude information of multi-symbol numbers.

Importantly, it was shown that 2nd graders who just learned about multi-digit numbers were observed to process them sequentially from left to right starting at leftmost digit pair (e.g., tens, Nuerk et al., 2004). In contrast, 3rd and 4th graders exhibit both sequential and parallel processing of multi-digit numbers depending on task difficulty, which corresponds to a mixed sequential and parallel processing mode (Nuerk et al., 2004; Mann et al., 2011). With increasing experience, 5th graders finally showed parallel processing of multi-digit numbers. Thus, only with increasing experience children process multi-digit numbers in a parallel way.

As such, it seems plausible that 6th graders in the present study who just learned about the concept of multi-symbol (i.e., negative) numbers did not yet process these in parallel but used a rather sequential strategy.

This would suggest that in heterogeneous number pairs the comparison of the polarity signs should be sufficient for decision making, whereas the magnitude of the digits should not have to be compared at all. In fact, we found evidence for such a shortcut strategy for the mixed-sign number pairs (e.g., -8 vs. +3) in the digit-direction congruency analysis. Importantly, incongruent mixed sign pairs did not differ from congruent mixed sign pairs neither in RT nor in error rates. Thus, it might be possible that 6th graders used this shortcut strategy throughout the mixed sign pairs and, in turn, processed multi-symbol numbers in a sequential componential way. Thus, for incongruent mixed pairs, a sign shortcut strategy would lead to a fast and accurate decision, whereas in congruent mixed sign pairs the comparison of both components separately (e.g., polarity sign or digit) would lead to a fast and correct response. In this way, the non-decisive component may not necessarily interfere or facilitate processing when incongruent or congruent, respectively. For incongruent same sign pairs, the sequential strategy was not sufficient to come up with the correct result because they would also have to use a mirroring strategy. This may have led to slower and less accurate responses. Accordingly, all these strategies might have led to not finding the compatibility effect.

Another possible explanation why we did not find a sign-digit-compatibility effect might be that multi-symbol number pairs were presented simultaneously in the present study. Recently, Ganor-Stern et al. (2010) argued that of complex numbers such as multi-symbol numbers only the information actually needed for the task at hand will be processed. In simultaneously presented mixed sign number pairs (which were exclusively analyzed for the sign-digit compatibility effect), sequential processing of the first component (i.e., the polarity sign) would suffice to make a decision. Thus, the lack of observing a significant sign-digit compatibility effect might also be due to the simultaneous presentation of the to-be-compared number pairs.

However, previous studies showed that the compatibility effect for a specific numerical concept develops with increasing experience with this specific concept. As 6th graders just learned about the concept of multi-symbol numbers, it is in line with recent literature that we did not find a sign-digit compatibility effect yet – although it has been shown in adults (Huber et al., 2014). With increasing experience, the processing of multi-symbol numbers may also develop from rather sequential to more parallel processing of the components which is a prerequisite for the compatibility effect. In turn, when the sign-digit compatibility effect finally occurs, it reflects parallel processing of multi-symbol numbers. Thus, this indicates that there seems to be a general developmental trend from sequential to parallel processing of multi-symbol numbers driven by increasing experience with the respective numerical concept.

Limitations

We are well aware that the current study only represents a first step towards a more comprehensive understanding of spatial associations of multi-symbol numbers. Thus, several aspects need to be considered when interpreting the results.

First, we deliberately chose to exclude same number pairs (e.g., -3 vs. +3) from the experiment because we used a magnitude comparison and number magnitude is the same for same number pairs when ignoring the polarity sign. As such, no decision on whether a number is larger or smaller would have been possible. Therefore, we excluded these specific number pairs. However, in doing so, a typical OSSA-effect as found by Pinhas and colleagues (2014) could not be evaluated in the current study because the polarity sign was always entangled with the magnitude of the number. For this reason, however, we explicitly did not name the respective effect OSSA-effect in the present study, but rather referred to it as sign-direction congruency effect. Furthermore, as children seemingly processed multi-symbol numbers in a sequential way, a sign-direction congruency effect might have emerged every time children only processed the polarity sign for their decision, but not number magnitude. However, to disentangle this issue, further research is needed.

Second, it needs to be noted that numbers in the present study were presented in vertical spatial positions (i.e., an upper and a lower number) while responses had to be mapped onto the horizontal dimension (i.e., left and right). We are well aware that there are spatial-numerical associations for vertical directions (e.g., large is up; Ito & Hatta, 2004). However, to the best of our knowledge, in studies on vertical dimensions there is a spatial association with the response location (e.g., larger numbers are faster responded when response is up, e.g., Gevers, Lammertyn, Notebaert, Verguts, & Fias, 2006; Hartmann, Gashaj, Stahnke, & Mast, 2014; Ito & Hatta, 2004; Müller & Schwarz, 2007), but not with the stimulus location. We do not know of any study that showed a vertical SNARC effect for stimulus location. Even for the well-researched horizontal SNARC, effects of or for location are usually quite weak. For instance, a recent large-scale multi-lab RRR study (Colling et al., in-principle acceptance, registered report) suggests that the attentional SNARC (Fischer et al., 2003), in which attention is supposedly directed to certain horizontal locations, cannot be reliably replicated. For these reasons, we see no evidence from the literature suggesting that the present procedure of vertically presentation of numbers influenced the results into one or the other direction.

Third, it is important to mention that parts of our argument are based on null results. However, we evaluated the validity of the null effects reported using Bayesian analyses which allow for quantifying the bias for either null or alternative hypothesis. These results substantiate our interpretation of the null effects. Nevertheless, further evaluation is required in future studies.

Conclusion

In line with previous research, the present data indicated that directional SNAs develop and become more pronounced with increasing experience and age. A SNARC-like digit-direction-congruency effect for number magnitude was found in 6th graders whereas we did not (yet) observe a directional SNA for polarity signs (i.e., sign-direction congruency effect) at that age. Furthermore, we also did not observe a sign-digit compatibility effect. Hence, the magnitude of the irrelevant digit did not interfere with processing the polarity signs. Taken together, this indicates that 6th graders may not yet associate polarity signs with space and still process multi-symbol numbers sequentially rather than in parallel. This might be because 6th graders just learned about negative, and thus, multi-symbol numbers. As such, they may still lack sufficient experience with this numerical concept to allow for a spatial association of the polarity sign and parallel processing of the components of multi-symbol numbers.

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Studies of Section 2:

The temporal dynamics of number processing

Study 4: Mock, J., Huber, S., Klein, E., & Moeller, K. (2016). Insights into numerical cognition – Considering eye-fixations in number processing and arithmetic. *Psychological Research, 80 (3),* 334-359.

9 Study 4: Insights into numerical cognition – Considering eye-fixations in number processing and arithmetic[12]

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Abstract

Considering eye-fixation behavior is standard in reading research to investigate underlying cognitive processes. However, in numerical cognition research eye-tracking is used less often and less systematically. Nevertheless, we identified over 40 studies on this topic from the last 40 years with an increase of eye-tracking studies on numerical cognition during the last decade. Here, we review and discuss these empirical studies to evaluate the added value of eye-tracking for the investigation of number processing.

Our literature review revealed that the way eye-fixation behavior is considered in numerical cognition research ranges from investigating basic perceptual aspects of processing of non-symbolic and symbolic numbers, over assessing the common representational space of numbers and space, to evaluating the influence of characteristics of the base-10 place-value structure of Arabic numbers and executive control on number processing. Apart from basic results such as reading times of numbers increasing with their magnitude, studies revealed that number processing can influence domain-general processes such as attention shifting – but also the other way round. Domain-general processes such as cognitive control were found to affect number processing.

In summary, eye-fixation behavior allows for new insights into both domain-specific and domain-general processes involved in number processing. Based thereon, a processing model of the temporal dynamics of numerical cognition is postulated, which distinguishes an early stage of stimulus-driven bottom-up processing from later more top-down controlled stages. Furthermore, perspectives for eye-tracking research in numerical cognition are discussed to emphasize the potential of this methodology for advancing our understanding of numerical cognition.

9.1 Introduction

Generally, eye-tracking as a method to investigate the cognitive processes underlying task performance allows for conclusions about where the subject's interest and concentration is focused on (Duchowski, 2007). More specifically, the eye-mind and the immediacy assumption claim that the location of an eye-fixation reflects the spatial locus (i.e., what is processed at the moment), while the duration of a fixation indicates the time course of cognitive processing (i.e., how long it takes to process the information at the fixated position, e.g., Just & Carpenter, 1980; Rayner & Pollatsek, 1989; for a critical view see Irwin, 2004). Considering this, tracking participants' eye-fixation behavior allows for a more in depth investigation of the underlying cognitive processes as well as the use of strategies while solving the respective task at hand. Hence, considering participants' eye-fixation behavior extends other behavioral findings such as reaction times and error rates by monitoring cognitive processing on-line.

The eye-mind as well as the immediacy assumption based on reading research can easily be transferred to research in other content domains such as numerical cognition. Comparably to the matter of reading, eye-tracking in numerical cognition research enables the on-line monitoring of number processing. This literature review summarizes and discusses the existing studies which employed eye-tracking to investigate number processing. Specific interest is paid to the added value of considering participants' eye-fixation behavior in numerical cognition research.

First, we give a brief overview on the physiology of vision and the development of the eye-tracking methodology. In the main section, we then discuss that in numerical cognition research participants' eye-fixations are considered in a way that ranges from (i) investigating basic perceptual aspects of the processing of non-symbolic as well as symbolic numbers, over (ii) appraising the common representational space of numbers and space, and (iii) evaluating the influence of structural characteristics of multi-symbol numbers to (iv) investigating influences of executive control on number processing. Finally, these findings are integrated into a model specifying the temporal dynamics of number processing in solving the particular task at hand. We conclude with a discussion of the perspectives for eye-tracking in numerical cognition research highlighting the benefit of this methodology.

Physiology of vision

Before elaborating on how eye-fixation data can inform us about the cognitive processes underlying numerical cognition, a brief introduction into the physiology of the visual system may be helpful. Starting from outside the eye, light enters via the pupil, the respective image is turned upside down by the lens and projected onto the retina (see Figure 9.1). Light-sensitive cells (i.e., cones and rods) in the retina transduce the light into electrical signals which are then transmitted through the optic nerve to the visual cortex for further processing (e.g., Holmqvist et al., 2011). While only cones are sensitive to color vision and thus allow for high resolution vision, rods are responsible for dark-adapted or scotopic vision under dim light conditions. Cones are extremely over-represented in the fovea centralis. To see at high resolution, we therefore need to move the eyes so that the object of interest (i.e., a number) is centered in the fovea (e.g., Land & Tatler, 2009). The movement of the eye-ball is called a saccade. Saccades serve to shift the direction of gaze from one object in the visual field to another (e.g., Fuchs, 1967). During a saccade the visual system is more or less insensitive to external changes. That is, vision is reduced during saccades which is called saccadic suppression (e.g., Land & Tatler, 2009). However, most eye-tracking studies do not much focus on saccades. They rather consider what is called fixations. This is the state when the eye remains still (e.g., when reading a number). Fixations can last from some milliseconds up to several seconds (e.g., Rayner, 1998). It is assumed that the position of the fixation reflects the position where attention is drawn to and from which relevant information is extracted during the fixation (Holmqvist et al., 2011; see also Just & Carpenter, 1980; for further reading on the physilogy of vision, its neural substrates and visual perception in general, see Hendee & Wells, 1997, for instance).

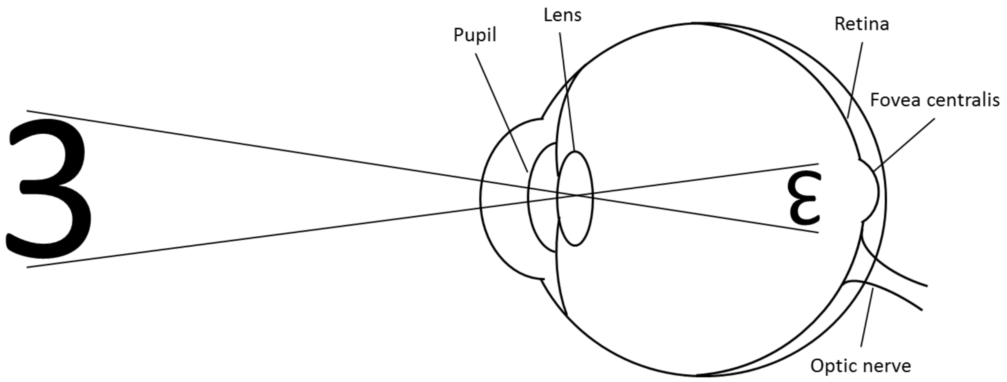

Figure 9.1: Schematic anatomy of the eye.

Development of the eye-tracking methodology

The first studies considering eye-movements during reading tasks were conducted by Huey (1898) and Delabarre (1898). To track participants' eye-movements, the authors fixated the head of the participants by using a bite bar and connected the eye with a kymograph by means of a lever fixed on a wire ring within a cast in front of the cornea. A solution containing 2 to 3% of cocaine was applied to anaesthetize the eyeball. Delabarre (1898) admitted "unpleasant effects" as a consequence due to the strain on the eye-muscles and other problems of this technique including the accommodation of the eye being affected by the cocaine (Delabarre, 1898, p. 574). Avoiding such unpleasant effects, Dodge and Cline (1901) introduced the idea of recording the reflection of an external light source from the cornea. Over decades this procedure has been developed to one of the dominating techniques of tracking eye-movements. In the 1950s, the use of a specific contact lens was employed to improve accuracy by attaching a mechanical or optical reference object onto the lens. However, the invasive nature of such techniques results in practical disadvantages (for a review on early eye-tracking methods see Robinson, 1968). Nevertheless, the use of such search coil methods allows for one of the most precise results of measuring eye-fixation behavior because of their high spatial and temporal resolution (Duchowski, 2007). Today, remote eye-tracking systems operate without any contact with the user and compensate for head movements within reasonable limits. Infrared LEDs generate reflections on the surface of the cornea which are used to find the eye in a camera image. As a result, the location of the center of the corneal curvature in space can be determined non-invasively. The spatial position of eye-fixations can be computed and thus monitored (for a detailed overview on the development of eye-tracking techniques see Duchowski, 2007).

Eye-tracking in cognitive tasks

Reading processes were the first to be examined by means of eye-tracking. Starting at the end of the 19th century, major insights into primarily perceptual processes were gained. In particular, the fast discontinuous movements of the eyes (i.e., saccades) were of specific interest besides fixation durations. In early studies from around 1880 to 1920, reduced sensitivity to visual input during saccades (i.e., saccadic suppression) and very short saccade latencies which suggest saccade programming in parallel with comprehension processes in reading were discovered (e.g., Dearborn, 1906; Dockeray & Pillsbury, 1910; Erdmann & Dodge, 1898). Moreover, the perceptual span (i.e., the number of letters to be processed within one fixation) was among the first to be studied (e.g., Rayner, 1975; Den Buurman, Roersema, & Gerrissen, 1981).

From the 1970s on, the increasing sensitivity of eye-tracking techniques allowed for a more specific investigation of the underlying cognitive processes in reading and other higher cognitive tasks (see Rayner, 1998 for a review). Besides reading research, research on scene perception as well as that on visual attention employed eye-tracking as a method to investigate underlying processes. Interestingly, scene perception and visual attention do not rely on linearly arranged material as is the case with reading. Thus, other underlying mechanisms involved in visual perception such as pre-saccadic attention (Zhao, Gersch, Schnitzer, Dosher, & Kowler, 2012), the preview benefit and eye-movement control were examined (for an overview, see Rayner, 2009). Since then, eye-tracking has provided a variety of different measures considering the number and duration of fixations (i.e., the duration of the first fixation on a stimulus, the overall number of fixations or the summed duration of all fixations on a stimulus) which allow for a differential evaluation of underlying cognitive processes. In particular, it is possible to differentiate between early stimulus-driven bottom-up and later top-down mediated processing by means of eye-tracking (Calvo, 2002). As repeatedly confirmed in reading research, measures such as first fixation duration (FFD) and gaze duration are sensitive to early stimulus-driven aspects such as the frequency of words (see Rayner & Pollatsek, 1989 for an overview). In contrast, the overall number of fixations and total reading times (TRT) on a stimulus are assumed to also reflect influences of later top-down processes such as plausibility judgments (e.g., Deutsch, Frost, Pelleg, Pollatsek, & Rayner, 2003; Joseph et al., 2008). This differentiation also applies to number processing (cf. Moeller, Fischer, Nuerk, & Willmes, 2009a). Therefore, this review aims at evaluating i) how eye-tracking is employed in the domain of numerical cognition and ii) in how far the potentials of eye-tracking can be exploited in numerical cognition research.

Over the last years, the number of studies in numerical cognition research using eye-tracking has steadily increased. Overall, we identified 45 eye-tracking studies: there were only 7 eye-tracking studies on numerical cognition before 2000, 3 more by 2004, another 10 more by 2009 and 25 more by 2015. Importantly, this trend seems to indicate the relevance of the results and insights gained by eye-tracking for our understanding of numerical cognition (for a short review, see Hartmann, 2015)

9.2 Basic perceptual aspects

An important advantage of recording participants' eye-fixation behavior in cognitive tasks is that the processing of the relevant task can be observed on-line. In contrast, looking at reaction times and error rates provides exclusively final information about the already completed task. In the following, we summarize and discuss those studies which primarily deal with basic perceptual aspects of the processing of non-symbolic numerosities, but also of symbolic numbers.

Perceiving non-symbolic numbers

It is assumed that humans share an approximate number system (ANS) with other species such as monkeys, but also parrots and fish. The ANS is thought to be innate so that already newborn (e.g., de Hevia, Izard, Coubart, Spelke, & Streri, 2014) or a few months old human infants are able to discriminate numerosities (e.g., Xu & Spelke, 2000; Lipton & Spelke, 2004; Xu, Spelke, & Goddard, 2005). Recently, it was reported that even fetuses in the last trimester are able to discriminate auditorily presented numerical cues (e.g., Schleger et al., 2014). Thus, perceiving non-symbolic numbers seems to be a basic perceptual process (see also Burr & Ross, 2008; Ross & Burr, 2010). Processing of non-symbolic magnitudes is usually investigated by quantification and enumeration tasks. Of particular interest in this respect is the concept of subitizing which denotes the ability to quickly identify the number of items in a small set of items (≤4) without counting. Subitizing was originally assumed to occur automatically and without involvement of attentional resources as a perceptually driven process. However, this was questioned by recent eye-tracking evidence (e.g., Sophian and Crosby, 2008). Moreover, the association of subitizing with typical and atypical numerical development in preschool and primary school children was substantiated by means of eye-tracking research.

In particular, Sophian and Crosby (2008) investigated the automaticity of subitizing by evaluating influences of pre-attentive (automatic) and attentional processes in an enumeration task. In this task, participants had to indicate the number of arrows (ranging from 1 - 6) pointing downwards, shown on a screen, under three conditions: in a first condition no distractors were included, whereas in a second and third condition oblique and vertical distractors, respectively, were included. In the no-distractor condition a reliably higher proportion of fixations targeted directly at the to-be-enumerated arrows in arrays of four or more items. This is in line with the assumption of automatic pre-attentive subitizing of arrays of three or fewer items. However, for oblique distractors this clear differentiation was not replicated. Instead, an evaluation of the time course of the fixation pattern indicated that for all distractor conditions and numerosities there is a phase in which target locations are fixated highly selectively indicating attentive processing. In sum, these data indicate “that all enumeration requires some attentional processing of target items, but the amount of attentional processing is markedly greater for numerosities of four or greater than for numerosities of three or fewer” (Sophian and Crosby, 2008, p. 407). Ceulemans and colleagues (2014) further evaluated the exact boundary between subitizing and counting range. They presented 9-month-old infants with sets of 4 vs. 8 dots and 1 vs. 4 dots. Looking times revealed that infants were successful in discriminating 1 from 4, but failed to discriminate 4 from 8 dots. According to the authors, this finding indicates that even sets of four may be subitized by an object-file system providing exact representations of numerosities up to four. In sum, these eye-tracking data substantiate the assumption that subitizing and counting reflect qualitatively different enumeration processes.

Back in 1891 Landolt claimed that counting accuracy is limited by small voluntary saccades. Evaluating this hypothesis, Kowler and Steinman (1977) examined counting accuracy for repetitive bar patterns and non-repetitive dot patterns while making either no or voluntary saccades. For repetitive patterns counting accuracy did not depend on saccadic eye-movements. Instead, counting was very successful when subjects made no saccades at all. However, in non-repetitive patterns saccades improved counting accuracy reliably. Because counting accuracy was higher when no saccades were made for repetitive patterns, only perceptual confusion rather than saccadic eye-movements seem to limit counting accuracy. Thus, when perceptual confusion was removed (such as in non-repetitive patterns by forming natural perceptual groups), saccades even increased counting accuracy.

Evaluating the association of subitizing with numerical development, Schleifer and Landerl (2011) investigated subitizing and counting abilities of typically (8-, 11-, and 14-years-old) and atypically developing children (8-, 9-, 10-years-old) in a dot enumeration paradigm (with 1 to 10 dots). The typical discontinuity between subitizing and counting was found in RTs as well as saccadic frequency in all age groups of typically developing children. This also held true for atypically developing children, although these children already in the subitizing range showed steeper RT slopes, indicating a dysfunctional subitizing mechanism. Moeller, Neuburger, Kaufmann, Landerl, and Nuerk (2009) further pursued this idea and assessed two boys with developmental dyscalculia (DD) on the same enumeration task while recording their eye-fixation behavior. In-depth evaluation of the eye-fixation data indicated that children with DD had to count already quantities of two and three items as reflected by steeper increasing numbers of fixations compared to their typically developing peers. Taken together, these eye-fixation data revealed that the deficiencies in basic non-symbolic tasks emerge from deficits at the level of automatic and parallel encoding of small non-symbolic quantities.

To sum up, eye-tracking data revealed that subitizing is not a purely automatic and pre-attentive process but seems to involve processes of attentional control (Sophian & Crosby, 2008). Moreover, Schleifer & Landerl (2011) substantiated the association of subitizing with typical and atypical numerical development. An evaluation of eye-fixation behavior in children with dyscalculia indicates that DD may indeed emerge (among others) from a deficit in subitizing and thus, the automatic and parallel enumeration of small set sizes (Moeller, Neuburger, et al., 2009).

Perceiving symbolic numbers

Early visual processes in perceiving symbolic numbers include the recognition of digits as reflecting numerical information (e.g., Dehaene & Cohen, 1995) and later on the reading of multi-digit numbers. In this sense, some eye-tracking studies investigated these basic perceptual aspects of symbolic numbers such as the processing speed of symbolic digits as well as the reading time of numbers.

Processing speed

Milosavljevic, Madsen, Koch, and Rangel (2011) were interested in early visual processes in number comparison. Here, the authors investigated the maximum speed at which individuals can make single-digit magnitude comparisons by means of a saccade to the left or right. They found that it took participants, on average, 306 ms to make these decisions with high accuracy. Interestingly, this was identical for "larger than" and "smaller than" comparisons. These results "suggest that the brain contains dedicated processes involved in implementing basic number comparisons that can be deployed in parallel with processes involved in low-level visual processing" (Milosavljevic et al., 2011, p. 1).

Reading time

One of the most basic information which can be derived using eye-tracking is the reading time for numbers. First experiments investigating number reading evaluated the influence of syllable length. In this context, Pynte (1974) found that the gaze durations on two-digit numbers increased with the syllable length of the number names. This result was further specified by Gielen, Brysbaert, and Dhondt (1991) who found that syllable length only affects gaze durations when the numbers have to be recalled. However, when participants had to decide whether the central one of a number triplet was the arithmetic mean of the two outer numbers, syllable length did no longer influence gaze durations. Instead, they found that gaze durations depended on the size of numbers. Brysbaert (1995) further examined whether the size of numbers or syllable length influences gaze durations. Additionally, he investigated the role of the frequency of a number. Brysbaert (1995) found that number recognition is facilitated after processing a number located close on the mental number line as compared to a number at a more distant location on the mental number line. Further, the increase of reading times with number size might be due to a frequency effect similar to the one found for word frequency. This is in line with the finding that the frequency of a number decreases the larger it gets (Dehaene & Mehler, 1992). Moreover, the influence of syllable length on reading times was again restricted to experiments where participants had to recode numbers from Arabic into auditory-verbal notation.[13]

In sum, this indicates that not only the numerosity of non-symbolic quantities but also the magnitude information of symbolic numbers is encoded in early perceptual stages because these numerical characteristics influence participants' eye-fixation behavior. In number reading, reading

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[13] Besides the reading times of numerals, eye-tracking was also employed to investigate the readability of different number formats which seem to differ with regard to their comprehensibility. Rello, Bautista, Baeza-Yates, Gerv, and Herv (2013) found that participants with dyslexia improved in text comprehension when digits and percentages were used instead of number words and fractions, respectively.

times increase with number size due to the word frequency, whereas the influence of the syllable length is restricted to tasks where numbers have to be recalled verbally (Brysbaert, 1995; Gielen et al., 1991). That is, semantic attributes are assigned in an early processing stage.

9.3 A common representational space of numbers and physical space

Eye-tracking also allows for a more thorough investigation of findings specific to the domain of number processing by providing in-depth information on particular processing steps and characteristics of numerical representations. In particular, the association of numbers and physical space (e.g., Fischer & Shaki, 2014 for a review) was substantiated by the added value of considering participants' eye-fixation behavior in numerical cognition research.

Attentional shift

The mental representation of numbers is often described by the metaphor of a mental number line on which numbers are aligned in ascending order (Restle, 1970). In Western cultures this mental number line is spatially oriented from left-to-right (e.g., Göbel, Shaki, & Fischer, 2011 for a review) meaning that small numbers are associated with the left side in space and larger numbers are associated with the right side in space. This is supported by a variety of empirical findings (e.g., Fischer & Shaki, 2014 for a review) – among others the Spatial-Numerical Associations of Response Codes (SNARC) and the Operational Momentum (OM) effect. The SNARC effect (e.g., Dehaene, Bossini, & Giraux, 1993) reflects that in parity judgement or magnitude comparison smaller numbers were found to be responded to faster by the left hand while larger numbers were responded to faster by the right hand. This is in line with the orientation of the mental number line. Furthermore, the OM effect generalizes the idea of a left-to-right oriented mental number line to the case of mental arithmetic. It provides an explanation for the finding that addition results were observed to be systematically overestimated while subtraction results were systematically underestimated (e.g., McCrink, Dehaene, & Dehaene-Lambertz, 2007). Following the rationale of the OM effect this pattern originates from the direction of "movements" on the mental number line implied by the respective operation: Adding two numbers results in a larger number located further to the right on the mental number line, whereas subtracting one number from another results in a smaller number located further to the left on the mental number line (Klein, Huber, Nuerk, & Moeller, 2014). Thus, addition induces a rightward bias on the mental number line whereas subtraction elicits a leftward bias on the number line. This finding further supports the hypothesis of attentional shifts along the mental number line to underlie the OM effect. Pinhas and Fischer (2008) further suggested that OM reflects a combined bias of spatial activation from operands, operator, and result size (see for discussion Hubbard, 2014). Taken together, both the SNARC and the OM effect indicate a systematic association of numbers and space which seems to induce respective shifts of spatial attention elicited by the processing of number magnitude or the execution of arithmetic operations (but see Fattorini, Pinto, Rotondaro, & Doricchi, 2015). Importantly, such manifestations of the mental number line have not only been investigated by manual responses but also by means of eye-tracking, gaining additional insights into the underlying mechanisms of the association of numbers and space.

SNARC-like effects

Previous findings have shown the SNARC effect using manual response methods (e.g., Wood, Willmes, Nuerk, & Fischer, 2008 for a review and meta-analysis). Yet, apart from manual classification data, Fischer, Warlop, Hill, and Fias (2004) observed a saccadic SNARC effect. Saccadic eye-movements to the left or the right as responses in a parity judgment task were recorded. Here, they found that a saccade to the right was initiated faster in response to a large number whereas a saccade to the left was faster in response to a small number. Besides this horizontal saccadic SNARC effect, these findings were replicated when participants were asked to indicate the parity of a single-digit number by upward versus downward saccades (Schwarz & Keus, 2004). In sum, these qualitatively and quantitatively similar SNARC effects for horizontal and vertical saccadic eye-movements support the idea of numbers being able to induce an attentional shift along the mental number line and, thus, a spatial representation of number magnitude (for spontaneous ocular drifts induced by auditory number presentation, see Myachykov, Ellis, Changelosi, & Fischer (in press) in this issue).

Besides symbolic digits, such a saccadic SNARC was also observed for non-symbolic magnitudes as well as the physical size of non-numerical cues. In a study by Bulf, Cassia, and De Hevia (2014) participants had to make a saccade to a target on the left or the right side of the screen after being presented with a small or large numerical cue (i.e., a dot pattern or digit) or a non-numerical cue (i.e., a physical shape) of differing size. Targets on the left were detected faster when preceded by either small numbers (dots or digits) or small-sized shapes while targets on the right were detected faster when following to large numbers or large-sized shapes. The results suggest that number and physical size spontaneously map onto an oriented space. Hence, this automatic association induces attentional shifts. In a follow-up study, Bulf and colleagues (2015) investigated the origins of the mapping between number magnitude and oriented spatial codes. In this study, 8- and 9-month-old infants were presented with a visual target either on the left or the right side of the screen after the onset of a small- or large-magnitude cue (i.e. dots or physical shape). The fixation time of the infants on the target was measured. They found that infants were faster at detecting targets on the right following large-magnitude cues and targets on the left following small-magnitude cues. This means, non-symbolic numerosities such as sets of dots induce attentional shifts towards a peripheral region in space already in infants. This provides further evidence for a left-to-right oriented spatial dimension of magnitude representations already during the first year of life.

This argument is further supported by the results of Ruiz Fernández et al. (2011) who examined whether number magnitude affects a person's eye-movement in a free-choice task. For this, two pictures of human faces were presented simultaneously on either side of the screen after presentation of a number in the middle of the screen. Participants were then asked to explore the screen after the presentation of the number. An evaluation of the first fixations on the faces confirmed that number magnitude affected gaze direction with by more prominent first fixations on the left after the presentation of a small number cue and on the right after presentation of a large number cue.

Furthermore, Loetscher, Bockisch, Nicholls, and Brugger (2010) evaluated whether it was possible to predict the size of the next number before it was spoken from tracking their eye-movements during a random number generation task. For this, participants were asked to produce 40 numbers between 1 and 30 in a random sequence while the positions of their eye-fixations were recorded. Importantly, the authors observed that both horizontal and vertical changes in eye position reliably predicted the magnitude of the next number to be produced by the participants. That is, leftward changes of eye positions were associated with the next number being smaller than the previous one, whereas a next number larger than the preceding one was associated with rightward changes in eye-positions. Furthermore, also the physical extent of changes in eye-positon was associated with number magnitude: physically longer saccades predicted a marked change in the size of the next number, while small changes in eye-position were associated with the next number being of comparable magnitude. Thus, not only the direction but also the physical extent of changes in eye-position predicted changes in the magnitudes of the numbers to be produced next. This suggests a strong association between eye-movements and the processing of the number magnitude (for the influence of saccadic eye movements and smooth pursuit on number processing, see Ranzini, Lisi, & Zorzi, (under review) in this issue)

Importantly, the observed influence of number magnitude processing on eye-fixation behavior reflects a spatial-numerical association (SNA) following the dominant reading direction of participants (i.e., left-to-right). However, because the respective SNAs were already found in preliterate children, they cannot be driven exclusively by participants' own reading experience. To account for SNAs in preliterate children, Nuerk and colleagues (2015) proposed several mechanisms driving directional SNAs even before formal reading instruction has started. For instance, observational learning, such as monitoring adult reading behavior as well as pretending reading and writing, may induce spatial-numerical directionality in preliterate children (e.g., Dobel, Diesendruck, & Bölte, 2007; Dooley, 2010). However, SNAs were even observed in infants (e.g., Bulf et al., 2015), and thus, might reflect an innate trait of human cognition (cf. de Hevia, Girelli, & Cassia, 2012; see also Macchia Cassia, McCrink, De Hevia, Gariboldi, & Bulf, (under review) in this issue). This argument is substantiated by recent results indicating that besides human infants, even 3-day-old domestic chicks, familiarized with a target number (i.e., 5), associate smaller numbers (i.e., 2) with the left and larger numbers (i.e., 8) with the right side in space (Rugani, Vallortigara, Priftis, & Regolin, n.d.). Thus, findings from human infants and non-human species suggest that SNAs may also be due to an innate, shared neuroanatomical representation of both numbers and space (Dehaene, 2004), which might be strengthened by cultural and educational experiences (for further evidence of a shared neuronal representation of numbers and space, see section 3.2).

Moreover, for specific SNAs such as the SNARC effect there is recent evidence suggesting that they may result from working memory processes rather than reflecting a long-term association of numbers and space. In this context, it was observed that the serial order of numbers is represented in a spatial dimension. Thus, van Dijck and Fias (2011) found that the retrieval of serially-ordered information from working memory seems to determine the association of numbers and space, with items towards the beginning of a sequence being associated with the left and items located towards the end associated with the right side in space. Rinaldi and colleagues (2015) evaluated whether serial order processing in working memory involves overt visuospatial attentional search. For this, participants were asked to memorize a sequence of 5 single digits (i.e., 5, 9, 3, 2, 6). Participants' spontaneous eye-fixation behavior during verbal reproduction of the sequence revealed leftward eye-movements when a digit from the beginning of the to-be-memorized sequence and rightward eye-movements when a digit towards the end of the sequence had to be retrieved. Thus, SNAs might originate from processing of serially-ordered information in working memory (J.-P. van Dijck, Abrahamse, Majerus, & Fias, 2013). However, there is also evidence suggesting that such working memory driven short-term associations between numbers and space co-exist with long-term representations indicating a left-to-right ordered representation of number magnitude (Ginsburg & Gevers, 2015).

Spatial biases in mental arithmetic

Loetscher, Bockisch, and Brugger (2008) further investigated whether attention orienting along the mental number line is reflected by eye-movements during a number bisection task. For this, ascending (i.e. 1-7) and descending (i.e. 7-1) single-digit number pairs were presented auditorily and participants had to indicate which number goes "halfway between x and y?" while changes in their eye-position were measured. Larger leftward eye-movements to number pairs presented in descending compared with ascending order. This suggests that the search for the number halfway between two given numbers is accompanied by systematic horizontal eye-movements, most probably along a left-to-right oriented number line.

Klein, Huber, Nuerk, and Moeller (2014) examined the cognitive processes underlying the OM effect by evaluating participants' eye-fixation behavior in addition and subtraction problems where the results had to be located on a given number line. Here, addition was associated with a spatial bias towards relatively larger numbers, whereas subtraction induced a bias towards relatively smaller numbers. This means, addition was associated with eye-movements to the right, whereas subtraction was accompanied by eye-movements to the left on the given number line. Importantly, such operational momentum biases were found not only in participants' estimations of the location of the results on the number line but also for the location of participants' first fixation on the number line and the dominant direction of subsequent eye-movements along the number line. Klein et al. (2014) identified two processes involved in the OM effect: an initial anticipation process that provides a first estimate of the result, and a second corrective process to finally pinpoint a specific location on the number line. Importantly, these results also indicate that the influence of number magnitude on participants' eye-fixation behavior and attention orienting is not limited to implicit processing of number magnitude. It rather generalizes to actively manipulating numerical magnitude in addition and subtraction.

Interestingly, this was further emphasized by recent data of Hartmann, Mast, and Fischer (2015) who investigated spatial biases during mental arithmetic. The authors collected fixation data on a blank screen while participants solved verbally presented arithmetic problems. Generally, the authors observed more rightward gaze positions for increasing magnitudes. More specifically, gaze was directed further up during addition than subtraction (for a similar result on repeated addition, see Hartmann, Mast, & Fischer, (in press) in this issue). However, gaze positions indicated that this difference was induced by the operator, and not by the addition or subtraction process itself. This means, gaze position initiated after the onset of the operator was located more upward after the operator "plus" compared to "minus". This finding supports the existence of an operation sign spatial association (OSSA) leading to an attentional shift triggered by the operation sign (Pinhas, Shaki, & Fischer, 2014)

To sum up, employing eye-tracking in numerical cognition research allows for conclusions about mental representations of numbers since processing of a specific numerical task can be observed on-line. Processing numbers can influence domain-general processes such as attention shifting. Both a horizontal as well as a vertical saccadic SNARC effect were observed for symbolic and non-symbolic digits (Bulf et al., 2014; Fischer et al., 2004; Schwarz & Keus, 2004). That is, parity information is assigned at an early processing stage. Moreover, the automaticity of the attentional shift emphasizes the influence of numbers on eye-movements and further provides evidence for the concept of the mental number line. Importantly, the automatic retrieval of number-to-space translation indicates that semantic attributes are assigned at an early processing stage. Furthermore, the operation sign in addition and subtraction tasks likewise leads to a spatial bias (Hartmann et al., 2015b), whereas the directionality of the spatial-numerical associations depends on context (Klein et al., 2014).

However, when using eye-movements as indications of attentional shifts, it is important to note that most theoretical accounts on visual attention distinguish between overt and covert attention. Only shifts of overt attention from one object to another are accompanied by an overt eye-movement. In contrast, when attention is shifted covertly, no eye-movement occurs (Land & Tatler, 2009). Thus, covert attention shifts cannot be measured directly by means of eye-tracking. However, it is assumed that covert attention drives overt attention to targets of interest. That is, covert attention is first oriented to the target location, before a saccade is initiated to orient overt attention to the target location (e.g., Deubel & Schneider, 1996; Henderson, 1992; but see Klein, 1980). There is also psychophysical and neurophysiological evidence for such an association of covert and overt attention shifts (Hoffman & Subramaniam, 1995).

Towards neurofunctional evidence

The influence of eye-movements on number processing and vice versa suggests an at least partially common representation of numbers and eye-movements. Interestingly, this view is supported by both recent eye-tracking and functional Magnetic Resonance Imaging (fMRI) data. A first study arguing with the neural processing of numerical information to influence eye-movements was Irwin and Thomas (2007) – even though they did not collect neurofunctional data. These authors investigated the effects of saccades on number processing. One group of participants completed a magnitude comparison task, whereas another group completed a parity judgment task. Participants in both groups made either no, short, or long saccades during the respective task.

While saccade distance had no effect on the parity judgment task, the reaction times for the magnitude comparison task increased with saccade distance for saccades from right to left. The authors explained this by the involvement of the right parietal cortex in generating leftward saccades but also magnitude comparisons. Thus, cognitive suppression during saccades occurs as a result of interference within the dorsal stream. Thereby, these eye-tracking data support the view of an at least partially shared representation of number magnitude and saccades in the dorsal stream. Further evidence supporting this view comes from fMRI studies. For instance, Knops, Thirion, Hubbard, Michel, and Dehaene (2009) investigated the role of brain areas associated with spatial coding in mental arithmetic. For this purpose, they trained a multivariate classifier to infer the direction of an eye-movement (i.e., left or right) from fMRI data. Afterwards, the authors tested whether the classifier could differentiate between participants being engaged in either addition or subtraction based on their brain activation during these tasks. Activation for the saccade and the arithmetic tasks partially overlapped in the bilateral posterior superior parietal lobule (PSPL) where the classifier (trained for the saccade task) was indeed able to differentiate between addition and subtraction with a classification accuracy above chance: addition was associated with activation similar to that during rightward and subtraction similar to that during leftward saccades. These findings indicate that mental arithmetic is associated with attentional shifts on the mental number line even on the neural level. This evidence is further endorsed by earlier studies observing an overlap in brain activation associated with calculation, phoneme transcoding, and saccades in the left posterior IPS (Simon, Mangin, Cohen, Le Bihan, & Dehaene, 2002) revealing a topographical layout of eye, calculation, and language-related areas within the parietal lobe.

Evidence from both eye-tracking ("The effect of saccades on number processing," 2007) and fMRI (Knops et al., 2009; Simon et al., 2002) suggests an at least partially shared representation of numbers and eye-movements. This means that the bi-directional influence of eye-movements on number processing and vice versa may – at least partially – originate from overlapping neural correlates of number processing, saccade programming, and processing of physical space on the neural level (Knops et al., 2009).

The added value of considering participants' eye-fixation behavior in numerical cognition research to learn more about the underlying processing mechanisms is particularly relevant when it comes to the understanding of the structural principle of our Arabic number system.

9.4 Structural characteristics of numerical notations

The base-10 place-value system represents the structuring principle of our Arabic number system with specific relevance for our understanding of multi-digit numbers. That is, the position of an individual digit within a multi-digit Arabic number defines its numerical value (i.e., units, tens, hundreds, etc.) with the value increasing by the powers of 10 with each step to the left within the respective digit string. In numerical cognition research, the investigation of multi-digit numbers is of great interest since it reveals *how* numerical information of single digits is processed and integrated into the base-10 place-value structure. Moreover, investigating the processing of multi-symbol numbers with the aid of eye-tracking provides additional information about the source of emerging differences in multi-symbol number processing. Processing of multi-digit symbolic numbers is often investigated using number magnitude comparisons or mental arithmetic tasks because these allow for discerning a specific hypothesis about the way the single digit constituents of multi-digit numbers are processed. In the following, we will first elaborate on studies investigating place-value processing using magnitude comparison tasks before referring to mental arithmetic.

Processing multi-symbol numbers

Currently, there are three models describing the processing of multi-digit number magnitude (see Nuerk, Moeller, Klein, Willmes, & Fischer, 2011; Nuerk, Moeller, & Willmes, in press for reviews). The model of *holistic processing* (e.g., Dehaene, Dupoux, & Mehler, 1990) assumes a holistic representations of multi-digit numbers. That is, they are processed as integrated entity (i.e., 25), not retaining information on the base-10 place-value structure of the Arabic number system differentiating between units, tens, hundreds, etc. The latter is considered in models of decomposed processing. In these models, separate processing of units, tens, hundreds and so on is assumed. However, when processed in a decomposed manner, the single digits of a multi-digit number may be processed sequentially or in parallel. The former was proposed by the model of *sequential decomposition* of Poltrock and Schwartz (1984). In contrast to this, Nuerk and Willmes (2005) postulated the model of *parallel decomposition* of multi-digit numbers. Importantly, the unit-decade compatibility effect allows for differentiating between these models. In two-digit number magnitude comparisons, Nuerk, Weger, and Willmes (2001) observed that responses were longer and more error prone for unit-decade incompatible number pairs in which the overall larger number includes the smaller unit digit (i.e., 62_47 with 6>4 but 2<7), compared to unit-decade compatible pairs (i.e., 57_42 with 5>4 and 7>2). This indicated that tens and units were processed in a decomposed and parallel manner. Because overall distance was matched between incompatible and compatible number pairs, the compatibility effect is hard to reconcile with the notion of a holistic representation of multi-digit number magnitude. Additionally, sequential processing of multi-digit numbers should have resulted in a reversed compatibility effect: when matching overall distance, the distance of the tens digits is necessarily larger for unit-decade incompatible pairs (see Nuerk, Weger, & Willmes, 2002 for a mathematical elaboration). Thus, when starting to process the numbers at the tens position, incompatible number pairs should be responded to faster because of the larger distance of the tens digits. Moreover, as the decision on which number is the larger one can already be taken by comparing the tens digits, no influence of the unit digits would be expected.

In this context, Merkley and Ansari (2010) found that the ratio of two to be compared multi-digit numbers reliably influenced number magnitude comparisons. In particular, effects of ratio were found on the number of fixations as well as the duration of fixations with more and longer fixations as the ratio of the two to be compared numbers decreased (i.e., the numerical distance between the numbers decreased). Furthermore, participants made more saccades in large ratio trails compared to small ratio trials. Thus, these data reveal that the ratio of two numbers modulates participants' eye-fixation behavior. Because the ratio of two two-digit numbers considers the overall magnitudes of the two numbers (i.e., 25/76) and not the single digits, this finding may be interpreted as evidence in line with the holistic model.

However, this conclusion may be premature. Moeller, Fischer, Nuerk, and Willmes (2009b) further evaluated the presented models of multi-digit number processing (sequential, parallel, and holistic) by considering participants' eye-fixation behavior in a two-digit number magnitude comparison task discerning compatible and incompatible number pairs. Discouraging the sequential processing model, the authors observed that units were fixated more often than tens. The sequential model would have predicted more prominent fixation on the tens, because the comparison process should start and end here when the tens digits differ. Furthermore, unit-decade incompatibility led to a specific increase of fixations on the unit and a decrease of fixations on the tens digits indicating specific processing of the unit digit in unit-decade incompatible pairs – possibly to overcome the opposing decision bias caused by these digits. This existence of the compatibility effect in participants' eye-fixation behavior argues against a purely holistic processing of multi-digit numbers. Rather these data support the model of decomposed parallel processing of multi-digit numbers.

Meyerhoff, Moeller, Debus, and Nuerk (2012) extended the scope to processing of four- and six-digit numbers. The authors included compatible and incompatible digit pairs at all possible positions within the examined four- and six-digit numbers (i.e., 5781_4281, 3957_3942). They observed regular compatibility effects for six-digit numbers which indicated at least partially parallel processing. However, in line with the results of Poltrock and Schwartz (1984) response latencies increased the further to the right the first differing digit pair was to be found. Additionally, this was accompanied by more fixations on the decision relevant digit pairs irrespective of their position within the multi-digit number. Thus, manual classification and eye-tracking data clearly suggested “that comparing multi-digit numbers incorporates characteristics of both, sequential and parallel processing of the individual digits constituting multi-digit numbers” (Meyerhoff et al., 2012, p. 88). In particular, the authors proposed that numbers of more than three or four digits are separated into chunks of digits. Within these chunks digits are processed in parallel, whereas the chunks themselves are processed sequentially (for language influences on multi-digit number processing, see Bahnmueller, Huber, Nuerk, Göbel, & Moeller (in press) in this issue).

These findings on the processing of multi-digit numbers were recently generalized to also account for multi-symbol numbers by Huber, Cornelsen, Moeller, and Nuerk (2014). The authors evaluated the processing of positive and negative numbers in a magnitude comparison task. They observed a sign-decade compatibility effect. Analogous to the case of unit-decade compatibility, the number with the larger decade digit also had the larger, thus, positive polarity sign in sign-decade compatible number pairs (i.e., -53 vs. +97), whereas in sign-decade incompatible pairs the number with the larger decade digit had a small, i.e., negative polarity sign (i.e., -97 vs. +53). Longer reaction times for sign-decade incompatible compared to compatible number pairs indicated parallel decomposed processing of digits as well as the polarity sign. This interpretation was substantiated by an identical sign-decade compatibility effect found in the eye-fixation data. This effect indicated that participants’ fixation pattern differed between sign-decade compatible and incompatible number pairs.

Evidence on the processing characteristics of decimal fractions was provided by Huber, Klein, Willmes, Nuerk, and Moeller (2014) who recorded participants’ eye-fixation behavior in a magnitude comparison task. A previous study by Varma and Karl (2013) reported a smaller compatibility effect for two-digit decimal fractions (i.e., 0.37_0.52) than for two-digit integers (i.e., 37_52). Based on this, the authors suggested that decimal fractions and natural numbers are processed differently: processing a decimal fraction (i.e. 0.34) leads to the parallel activation of both the proportion referent (i.e. *0.34*) and the natural number referent (i.e. *34*) which, in turn, slows down performance. Huber, Klein, et al. (2014) disconfirmed this account. Their observation that participants fixated hundredth digits less than tenth digits revealed that decimal fractions were processed in a more sequential manner than two-digit numbers. Hence, the authors concluded that processing of natural numbers and decimal fractions can be accounted for by the same underlying mechanisms. This was further supported by the results of a computational modelling study in which a model of decomposed processing was able to replicate the empirical results.

Thus, magnitude comparison tasks using distinct numerical characteristics such as multi-digit numbers (Meyerhoff et al., 2012; Moeller, Fischer, et al., 2009b), multi-symbol numbers (Huber, Cornelsen, et al., 2014) as well as decimal fractions (Huber, Klein, et al., 2014; Huber, Moeller, & Nuerk, 2014) provide information about the processing of number magnitudes. The described eye-tracking data suggest that multi-digit numbers containing up to three digits are processed in a decomposed parallel way (Moeller, Fischer, et al., 2009a), whereas multi-digit numbers containing more than three or four digits are separated into sequentially processed chunks, while digits within these chunks are processed in parallel (Meyerhoff et al., 2012). Furthermore, the existence of the compatibility effect in eye-tracking studies provides evidence against a purely holistic processing since the eye-tracking data revealed selective encoding on the digit level (e.g., Moeller, Fischer, et al., 2009b; Huber, Cornelsen, et al., 2014). Further evidence for a decomposed parallel processing is additionally gained by a generalized model framework which detected the same underlying mechanisms in multi-digit numbers, positive and negative numbers as well as decimal numbers (Huber, Cornelsen, et al., 2014).

Processes involved in arithmetic

The structural characteristics of multi-symbol numbers and, thus, the base-10 place-value system, constitute the basis for more complex tasks such as arithmetic. For instance, in addition tasks a carry is needed whenever the sum of the unit digits of the summands is ≥10 (i.e., 6 + 9 = 15 in 36 + 19 = 55), whereas no carry is needed whenever the sum of the units is <10 (i.e., 3 + 4 = 7 in 13 + 34 = 47). Generally, when solving arithmetic problems specific procedures and strategies need to be applied (i.e., the carry operation in addition, multiplication first, etc.). Measuring participants' eye-fixation behavior while they solve arithmetic problems may help to understand the ongoing processes as it allows for an on-line monitoring of the calculation process. Interestingly, the first study investigating eye-fixation behavior in arithmetic by Suppes, Cohen, Laddaga, Anliker, and Floyd (1983) did not infer the ongoing calculation processes from recorded eye-tracking data. Instead, the authors first built up a procedural theory of eye-movements in arithmetic (i.e., addition and subtraction), which was then tested in an empirical study. Following their theory, there are four different eye-movements in arithmetic: forward (i.e., looking at the next displayed symbol), stayput (i.e., staying at a given location), backtracking (i.e., looking back to the preceding number), and skipping (i.e., skip over to the following symbol when it is already processed from the present point of view). In general, this theoretical approach was supported by the eye-fixation data of five participants. However, Suppes et al. (1983) admitted that known characteristics of eye-movements were not considered. Further, the processes described in their model seem too discrete regarding the more continuous processing of arithmetic problems. These weaknesses were overcome by a number of later studies that investigated processes underlying arithmetic in a more continuous manner. Here, the time course was considered by means of different eye tracking measures differentiating early bottom-up driven and later top-down mediated processing stages.

In this context, Moeller, Fischer, Nuerk, and Willmes (2009a) examined the influence of multiplicative relatedness and parity on the number bisection task. In this task, participants had to indicate whether the central number of a triplet (i.e., 21_24_27 vs. 21_24_28) also reflected the arithmetic integer mean of the given interval. Here, multiplicative relatedness indicates whether a triplet is part of a multiplication table or not (i.e., 21_24_27 vs. 21_25_29). In multiplicatively related triplets the automatic activation of multiplication fact knowledge facilitates the decision (H. Nuerk, Geppert, van Herten, & Willmes, 2002). In contrast, number parity plays a role for evaluating the overall bisection possibility of the triplet. Only when the first and the third number of the triplet are of the same parity there is an integer mean for this triplet (i.e., 21_24_29, correct mean would be 25 vs. 21_25_28, correct mean would be 24.5). In line with the assumption that multiplicative relatedness should reflect automatic bottom-up influences of multiplication fact knowledge, Moeller, Fischer, et al. (2009a) observed increased gaze duration for multiplicatively related triplets. On the other hand, influences of the parity manipulation were found in total reading times supporting the expectation that this manipulation should affect later processing stages as it requires the integration of information across numbers. [14]

Moreover, the sub-processes involved in addition were investigated by Moeller, Klein, and Nuerk (2011b) with a specific focus on the carry operation. In case a carry operation is needed, the tens digit of the unit sum has to be added to the sum of the tens digits to obtain the correct result [i.e., 26 + 17 = 43, for the units 6 + 7 = (1)3, for the tens 2 + 1 + (1) = 4]. Moeller et al. (2011b) recorded participants' eye-fixation behavior in a two-digit addition verification task. In addition to increased RTs for addition problems requiring a carry, the eye-fixation data indicated that there are three processes underlying the carry effect in addition: (i) the unit digits of the summands are summed already in first pass encoding. This was indicated by the fact that first fixation durations on the unit digit of the second summand increased with the sum of the unit digits. This provides the critical information for (ii) the recognition of whether a carry operation is required (for unit sums ≥10) or

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[14] While further investigating the mental representation of arithmetic facts, Zhou, Zhao, Chen, and Zhou (2012) employed horizontal electrooculography (HEOG) in single-digit addition and multiplication problems. This method only provides information about the horizontal direction (i.e., left/right) of eye-movements. In their HEOG data the authors found converging evidence for a preferred operand order in the representation of arithmetic facts. In particular, the HEOG data indicated that participants preferentially fixated the larger operand first. Again relying on HEOG, Yu, Liu, Li, Cui, & Zhou (in press, in this issue) showed that the direction of eye movements in mental arithmetic is influenced by the relative magnitude of the operands.

not (for unit sums < 10). Finally, (iii) the execution of the actual carry procedure was associated with more refixations of and increasing total reading times on the unit digits on the summands indicating their specific relevance for the carry operation. Additionally, the need for a carry also increased TRT on the tens digit of the result. The authors interpreted this to reflect the additional processing demand due to the need of the carried one to be added to the sum of the tens digits to come to the correct result.

Partially replicating and extending these results Moeller, Klein, and Nuerk (2011a) investigated developmental changes in two-digit addition performance by comparing addition performance and eye-fixation behavior of third-grade children and adults in a choice reaction time paradigm with two solution probes. In line with Moeller et al. (2011b) the authors observed a specific increase of TRT on the unit digits for problems requiring a carry operation for both children and adult participants. However, despite these similarities there were also differences found between the addition process of children and adults. Even though the need for a carry had a similar effect on the fixation pattern of children and adults, the eye-fixation pattern of children seemed less specific. In general, adults showed a more goal-directed fixation pattern favoring the unit digits over the tens, whereas children fixated longer on the tens of the summands indicating an influence of experience and automation regarding the underlying calculation processes.

Furthermore, Landy and colleagues (2008) evaluated whether attention is allocated faster to multiplication than to plus signs in multi-term arithmetic problems. At the same time, they were interested in whether narrow spaces draw the gaze comparably to multiplication signs. In this study, they presented students with simple two-operator arithmetic problems (addition or multiplication) in four different spacing conditions (i.e. narrow-wide: 2*3 + 4; wide-narrow: 2 * 3+4; wide-wide: 2 * 3 + 4; narrow-narrow: 2*3+4). Participants tended to focus early in a trial on narrow spaces and multiplication signs, and to move toward wider spaces and addition signs towards the end. This means, narrow spacing and multiplication have similar effects on attention.

Apart from evaluating cognitive processes in mental arithmetic on Arabic digits, eye-tracking was also employed to investigate cognitive processes in solving arithmetic word problems. For instance, De Corte and colleagues (1990) investigated the influence of the semantic structure of one-step addition and subtraction word problems on the eye-fixation pattern of second graders. Pupils spent more fixation time on the words in complex problems compared to simple problems. Additionally, longer response times of children with only low math abilities originated from more time spent on rereading the problem. These children also fixated the words as well as the numbers considerably longer in the rereading phase than did their peers with relatively higher math abilities.

The authors suggest that the longer duration of rereading the problem by low-ability pupils' was mainly due to computational activities.

Furthermore, Hegarty and colleagues (1992) investigated the processing of word problems containing a relational term that is inconsistent with the required operation (e.g., the term *less* requiring addition: "At ARCO gas sells for $ 1.13 per gallon. This is 5 cents less per gallon than gas at Chevron. If you want to buy 5 gallons of gas, how much will you pay at Chevron?"). For this, students' eye-fixations were recorded as they read arithmetic word problems. Students needed more time for inconsistent than consistent problems. Further, this additional time was associated with the integration/planning stages of problem solving as reflected by more rereadings of previously fixated words for inconsistent than for consistent problems.

Moreover, participants' eye-fixation behavior was also considered to investigate differences in the application of strategies between individuals. Green, Lemaire, and Dufau (2007) evaluated the influence of age on the use of a "unit-" or "hundred-strategy" in three-digit addition (i.e., whether participants start calculating from the unit digits or the hundred digits). In a choice condition, participants should select a strategy on their own, whereas in a no-choice condition the to-be-used strategy was instructed. The collected eye-fixation data confirmed that participants used the instructed strategy in the no-choice and the reported strategy in the choice condition. Furthermore, the eye-fixation data also revealed that young adults distinguished more clearly between the two strategies whereas older adults chose the strategies less adaptively (for influences of practice on strategies in multiplication, see Ganor-Stern & Weiss (accepted for publication) in this issue).

In a similar context, Schneider and colleagues (2012) investigated the role of syntax in arithmetic expressions. In their study, participants were presented with arithmetic expressions consisting of multiple operations organized by parentheses [i.e. left-branching: ((3+2)-1)+4) or right-branching: 4+(1-(3+2))]. The position of the initial fixation on the expression was identical for all expressions reflecting a bias towards a start point on the left of the expression – possibly driven by reading experience. However, in right-branching expressions participants quickly corrected their fixation position towards the operation to-be-performed first. In a second experiment, Schneider and colleagues (2012) embedded the first operation in the center of the arithmetic expression [e.g., 4+((1+2)-3)]. Additionally, they included expressions where the syntactic structure was partly implied by the operator [i.e. "multiplication first": 2+(4+5x3)]. Again, they found a leftward bias for the initial fixation which is corrected rapidly to accommodate the syntactic structure of the expression. Importantly, this rapid extraction of syntax did not necessarily require explicit structuring such as parentheses but also occurred rapidly using implicit rules such as "multiplication first". This means that syntax in arithmetic can be extracted automatically and in parallel.

To sum up, eye-movements during arithmetic indeed involve forward and backward eye-movements as well as fixations on and skipping of symbols as suggested by Suppes et al. (1983). However, recent studies provide more in-depth and wide-ranging evidence for the underlying processes in mental arithmetic due to results of eye-tracking studies. Here, early bottom-up processes indicate the retrieval of arithmetic fact knowledge, while late top-down mechanisms reflect the consideration of additional information (Moeller, Fischer, et al., 2009b). Furthermore, in addition tasks with carry problems early and late encoding processes seem to partially interact (Moeller et al., 2011b). Finally, eye-tracking evidence suggests that children present a lack of experience and automation regarding the processing of place-value information, which is necessary to complete procedural rules such as the carry operation (Moeller et al., 2011a). The latter seems to be of specific interest when investigating influences of solution strategies and their adaption in numerical tasks and development.

9.5 Influences of solution strategies and their adaption to number processing

Eye-tracking seems particularly useful to investigate how specific solution strategies and their adaption by domain-general processes such as executive control impact on number processing are. This is the case because it allows for an on-line monitoring of the solution process. In this sense, structural place-value characteristics of multi-digit numbers were used to evaluate adaption of solution strategies. On the other hand, the structure of dot patterns was found to influence the processing of non-symbolic magnitudes. Finally, participants' eye-fixation behavior has been considered to differentiate between the application of distinct strategies in number line estimation.

Influences of cognitive control

Cognitive control is the appropriate adjustment in perceptual selection, response biasing, and on-line maintenance of contextual information (e.g., Botvinick, Braver, Barch, Carter, & Cohen, 2001). Interestingly, in recent years influences of cognitive control on number processing have gained increasing research interest (e.g., Macizo & Herrera, 2011, 2013). In particular, the manipulation of item properties was often used to investigate influences of cognitive control on number processing. This means adaptation processes of the cognitive system were measured with respect to the changes in stimulus material. For instance, in a number magnitude comparison task Huber, Cornelsen, et al. (2014) manipulated whether heterogeneous number pairs (i.e., -53 vs. +97) and homogeneous number pairs (i.e., +53 vs. +97) were presented in separate blocks or intermixed.

For the heterogeneous pairs, the authors found a larger sign-decade compatibility effect for the mixed condition accompanied by a specific increase of fixations on the tens digits. This reflects that participants needed to consider both the polarity sign and the tens digits for their decision on heterogeneous pairs in the intermixed condition because it was not possible to infer the decisive position beforehand: in the homogeneous pairs, the tens digit is decisive, whereas in heterogeneous pairs the polarity sign is decisive. With 50% of both items being presented in an intermixed manner, it is most beneficial to consider equally the polarity sign and the tens digit. In turn, this increases the influence of the irrelevant tens digit in the heterogeneous pairs. This is reflected by a higher sign-decade compatibility effect and a higher number of fixations on the tens digit to overcome this interference. When heterogeneous and homogeneous pairs are presented in separate blocks, it is possible for participants to adapt to the respective decision relevant position, which leads to a reduced or even absent sign-decade compatibility effect.

Similarly, it was observed that the unit-decade compatibility effect is modulated by the percentage of same-decade filler items (i.e., 34_37) in the stimulus set. Again, it is argued that the inclusion of such filler items increases the decision relevance of the unit digits in the stimulus set (as within-decade fillers do not differ at the tens digits). In turn, this should increase unit-based interference in between-decade filler pairs resulting in a more pronounced unit-decade compatibility effect the more within-decade fillers are included in the stimulus set (Macizo & Herrera, 2011, 2013). Importantly, Huber, Mann, Nuerk, and Moeller (2014) showed that comparableto the sign-decade compatibility effect an increase of the unit-decade compatibility effect with an increasing percentage of within-decade filler pairs was accompanied by a shift of fixations towards the increasingly decision relevant unit digit. While the tens were fixated longer than the units when only 25% fillers were included in the stimulus set, this was reversed when the set included 75% fillers. This finding suggests reliable adaptation to stimulus set characteristics, and thus, influences of cognitive control in number processing.

Apart from multi-symbol numbers, influences of cognitive control have also been documented by means of eye-tracking for processing of fractions. In this context, Huber, Moeller, and Nuerk (2014) examined the influence of cognitive control on the processing of different fraction pairs with same nominators, same denominators, or those without common components under different blocking constraints (i.e., intermixed or in separate blocks) in a magnitude comparison task. Participants processed fractions with common components faster than fractions without common components because they focused their fixations specifically on the decision-relevant component. This effect was even more pronounced when the different fraction pairs were presented in separate blocks, because such blocking allows for anticipating the decision-relevant component in advance. In line with recent studies, this suggests that fractions are processed componentially, provided it is possible to identify the relevant components. When this is hardly possible or not possible, the overall magnitude of a fraction seems to be computed. Importantly, participants adapted their fraction processing to the experimental context. Thus, this provides further evidence for the influence of cognitive control in number processing.

Taken together, multi-symbol number processing requires cognitive control. This was reflected in participants' eye-fixation behavior by a larger sign-decade compatibility effect for the comparison of positive and negative numbers (Huber, Cornelsen, et al., 2014), by modulating the compatibility effect in multi-digit numbers by means of different types of filler items and percentages (Huber, Mann, et al., 2014) as well as by fraction processing (Huber, Moeller, et al., 2014). Participants adapt their processing strategy to the experimental context and focus on task-relevant aspects, which demands cognitive control.

Strategies in non-symbolic number tasks

Using distinct structures in dot patterns (canonical vs. random), Gandini, Lemaire, and Dufau (2008) were interested in the strategies applied by younger and older adults in an approximate quantification task. In this study, participants had to estimate the number of items in sets of 4 to 79 dots. Besides participants' performance, the authors collected participants' verbal strategy reports as well as their eye-fixation behavior. Both young and older adults used the same set of strategies, although to a different extent. An evaluation of participants' eye-fixation data confirmed the expected different encoding depending on the applied strategy. When using a benchmark strategy (i.e., scanning the stimulus and then comparing it to an internalized standard), participants started with saccades of small amplitudes to gradually encode configurations of dots followed by larger saccades to scale their initial estimate up to the entire stimulus. On the other hand, when applying an anchoring strategy, participants started with large saccades to broadly explore the collection of dots. In this way, subgroups of dots are identified which are then enumerated (via counting), followed by a visual estimation of the remaining dots. Thus, the quantification of larger numerosities requires the application of specific strategies which involve different encoding processes depending on the respective strategy.

Godau and colleagues (2014) investigated whether fixation patterns in a marble estimation task influenced performance in an arithmetic task. To pursue this issue, the authors manipulated the location of the marbles so that one group of elementary school children had to make long-range eye-movements whereas another group of children did not need long-range eye-movements to differentiate between few and many marbles. Afterwards participants had to solve addition problems that contained shortcut options based on the commutativity principle. Surprisingly, the horizontal saccade distance for the commutative problems was lower for the long-range eye-movements group. Yet, the differences in fixation patterns did not lead to differences in arithmetic performance.

Strategies in number line estimation

Estimating the location of a given number on a number line of which only the start and endpoint are specified (i.e., 0 and 1000) is a commonly employed task to assess the spatial representation of number magnitude (e.g., Siegler & Opfer, 2003). However, in recent years there was a controversial debate on what is actually measured by this task because there is accumulating evidence suggesting that number line estimation performance may not reflect numerical estimation but rather the application of proportion judgement strategies (e.g., Barth & Paladino, 2011). The evaluation of participants' eye-fixation behavior during number line estimation has been an additional source of evidence for this controversy.

With regard to the application of proportion-judgement strategies, Sullivan, Juhasz, Slattery, and Barth (2011) recorded the eye-fixation pattern of adult participants while they solved a number line estimation task. Substantiating the prominent application of proportion judgement strategies, the authors observed that participants preferentially fixated possible reference points (i.e., start, end, and midpoint of the number line). Furthermore, the final marking of the estimated position of a target number was preceded by an increase of fixations at or near the finally marked location. In the end, the position of the first fixation on the number line was reliably influenced by the magnitude of the target number indicating an internal calibration of the first saccade onto the number line.

To evaluate the development of numerical competencies, Schneider et al. (2008) investigated number line estimation performance in children from grade 1 to 3 by means of estimation accuracy and children's eye-fixation patterns. Grade-related increases of estimation competence were reflected in children's fixation patterns. With increasing grade level the proportion of fixations at or close to the correct location of a number increased. Interestingly, this fixation accuracy was closely related to children's actual estimation performance and – at least for grade 2 – also associated with children's addition performance. In line with the results of Sullivan et al. (2011), eye-fixations were distributed systematically over the number line with peaks of fixations at and around reference points (i.e., start, end, and midpoint of the number line) for all grade levels indicating the application of proportion judgement strategies. On the other hand, the observed decrease in fixation frequency with increasing magnitude of the target number indicated that a counting strategy was used frequently. In sum, these results indicate that eye-fixation patterns reflect the development of numerical competencies in primary school children.

This grade-related increase of numerical competence was investigated in more depth by Heine and colleagues (2010). The estimation data revealed a transition from estimation performance in first grade being accounted for best by a logarithmic function to being described best by a linear model in grade two. In addition to these estimation results, children's eye-fixation patterns indicated that an at least implicit understanding of the linear layout of the number line may already be present before this knowledge manifests itself explicitly and becomes observable in children's estimation patterns. That is, already in first grade the eye-fixation data was fit well by a linear model whereas this was not the case for the estimation data. Based thereon, the authors concluded that eye-fixation data provide insights into transitional phases of numerical development.

The fact that eye-fixation data reflects developments in number line estimation is of specific interest because it is known that children with DD show particularly poor performance when it comes to number line estimation. In an attempt to better understand why this is the case, van Viersen, Slot, Kroesbergen, van't Noordende, and Leseman, (2013) compared the eye-fixation behavior of a nine-year-old girl with DD with those of a control group of typically developing children in a number line estimation task. Eye-fixation behavior was clustered to reflect three different types of strategies: First, counting up from the starting point of the number line; second, counting down from the end point of the number line, and third, using the midpoint of the number line to start counting. In each of these three strategies there were fixations at the respective reference point followed by a series of fixations moving away from the reference point in the expected direction. Sequences that did not correspond to the predefined strategies were coded as undefined. In a next step, it was coded whether the respective strategy was functional or dysfunctional for the respective target number (i.e., for the target number 92 counting down from the endpoint 100 would be a functional strategy whereas counting up from 0 would be not). In addition to differences in encoding the target numbers, evaluation of the fixation patterns indicated that the child with DD applied much more dysfunctional strategies than did the children of the control sample (for similar results for a group study of children with mathematical learning difficulties, see van't Noordende, van Hoogmoed, Schot, & Kroesbergen (under review) in this issue). The authors suggested that "in line with [the] dyscalculia diagnosis, these results confirm the difficulties with spatially representing and manipulating numerosities on a number line, resulting in inflexible and inadequate estimation or processing strategies" (p. 1). Schot et al. (2015) replicated these results in a group study.

Thus, the accomplishment of number line estimation tasks is accompanied by the use of strategies in adults and children. In adults, the given target number affects the first fixation on the line. This indicates a precise number-to-space translation and the treatment of estimation tasks as instances of proportion judgment (Sullivan et al., 2011). In children, the developing number sense influences number line estimations. However, while behavioral data suggest a logarithmic pattern of representation in grade 1 which develops to a more linear pattern in grade 2 to 3, eye-fixation behavior indicates an implicit understanding of the linear number representation (Heine et al., 2010; Schneider et al., 2008). Estimation performance and eye-fixation behavior of children with DD reflect deficiencies in connecting number symbols to the appropriate magnitude and their location in space (Viersen et al., 2013).

Finally, there are also first studies considering participants' eye-fixation behavior in more complex arithmetical procedures. These shall be discussed in the following.

9.6 Complex mathematical procedures

Susac and colleagues (2014) examined students' strategies in simple equation solving. For this, equations consisting of three elements were presented (i.e., $x \cdot a=b$) together with a solution probe. Participants were asked to make *x* subject of the equation and to decide whether the presented answer was correct or incorrect. They had to indicate their response by looking to the left ("yes") or the right side ("no") of the screen. All participants improved their performance during the task. However, non-experts showed more fixations on the equation than experts. The authors suggest that experts developed a more efficient strategy because they knew where to look at.

Epelboim and Suppes (2001) recorded the eye-movements as three participants solved geometry problems posed with diagrams. Participants used highly redundant eye-movement patterns with multiple rescans of the same geometrical elements. These results suggest that geometrical elements from diagrams are added to visual working memory when they are scanned while newly added elements overwrite older elements.

Taken together, these studies present clear evidence that the evaluation of participants' eye-fixation behavior provides insights not only into the cognitive processes underlying more or less basic numerical tasks but is also meaningful when it comes to equation solving or geometry. However, future research is needed to further pursue this line of evidence.

9.7 Additional eye-related measures

Besides the method of directly tracking participants' eye-fixation behavior, there are several related measures that allow for drawing conclusions on underlying cognitive processes by observing characteristics of the eyes while completing cognitive tasks. In the following section, we will provide a brief overview of such measures (i.e., microsaccades, pupillometry and habituation) which have been considered to investigate numerical cognition.

Microsaccades

Microsaccades are described as rapid intra-fixational eye-movements that quickly bring back the eye to its original fixation position (Holmqvist et al., 2011). Microsaccades are involuntary, small-magnitude saccadic eye-movements. Yet, they have dynamic characteristics similar to those of saccades. Siegenthaler et al. (2014) investigated the effects of task difficulty on microsaccades during a mental arithmetic task with two levels of complexity. They found that microsaccade rates decreased and microsaccade magnitudes increased with increasing task difficulty. That is, microsaccades may serve as an additional indicator of the difficulty of numerical tasks.

Pupillometry

Additionally, pupil size can be highly informative about the difficulty of a task at hand. It was suggested that even small changes in pupil size are indicative of cognitive effort because there is a link between the ocular muscles and the neurotransmitter system controlled by the locus coeruleus in the brainstem (Hartmann & Fischer, 2014). Importantly, the locus coeruleus also plays a crucial role in attentional processes. Thus, pupillometry was argued to reflect the state of mind (Laeng, Sirois, & Gredeback, 2012). For the case of number processing Hess and Polt (1964) showed that pupillometry allowed for predicting problem difficulty in simple multiplication. That is, pupil size increased with problem difficulty. Additionally, there was an immediate drop in pupil size once the answer to a multiplication problem was given. For this, Hess and Polt (1964) suggest that the pupil response is a direct reflection of neuronal activity. Furthermore, Porter and colleagues (2007) used a pupil dilation measure to investigate the processing effort during a visual search and a counting task. The pupil dilated more during counting compared to the search task. Furthermore, the dilation pattern reflected an increased initial effort in the counting task - that is, counting requires from the start a strong locational memory component as compared to a search task. Importantly, pupillometry seems a promising method for future research as pupil size information can be recorded by most common eye-tracking devices in addition to fixation behavior (Hartmann & Fischer, 2014).

Habituation of looking time

Although not recording exact eye-fixation behavior, habituation paradigms focusing on looking times represent another valuable method to investigate processes underlying numerical cognition – in particular in children and infants. Using a habituation paradigm, Wynn (1992) showed that already 5-month-old infants represented numerical magnitude and were even able to perform simple additions and subtractions. In this study, children were presented with a single item in an otherwise empty display area. Afterwards, the item was hidden and a second item was brought into the area, in clear view of the infant. Thus, infants saw the operation of adding being performed but not the result (in this case the resulting two objects). Importantly, infants were observed to look longer at unexpected outcomes of simple arithmetic operations (i.e., only one object on the display after another one was added) than at expected ones (i.e., two objects on the display). The availability of such arithmetical abilities at the age of five months suggests an innate capacity to perform simple arithmetic operations (for a spatial bias in early arithmetic, see also Macchia Cassia, McCrink, De Hevia, Gariboldi, & Bulf (under review) in this issue). Also using a habituation paradigm, De Hevia, Girelli, Addabbo, & Cassia (2014) observed that 7-month-old infants already showed a preference for increasing magnitude displayed in a left-to-right oriented spatial arrangement. In their study, two groups of infants habituated to left-to-right oriented increasing or decreasing numerical sequences, respectively. Afterwards both groups showed higher looking times to new left-to-right oriented increasing sequences, but not to right-to-left oriented sequences. This again indicates an early disposition in humans to associate numerical order with a left-to-right spatial layout.

9.8 Conclusion

Synopsis of empirical evidence

The aim of the present review was to summarize and discuss the existing eye-tracking studies in numerical cognition research to evaluate the added value of eye-tracking as a method to investigate number processing. Importantly, the above review of the literature clearly indicates that eye-tracking not only allows for substantiating previous behavioral findings but also provides new insights into the processes underlying numerical cognition.

As regards basic perceptual aspects, eye-tracking confirmed the differentiation between subitizing for numerosities up to three or four and other enumeration processes for larger numbers when it comes to the processing of non-symbolic magnitudes (Schleifer & Landerl, 2011). However, considering participants' eye-fixation behavior also led to new insights into the underlying processes. In this context, Sophian & Crosby (2008) were able to show that – unlike hypothesized on the basis of RT data only – subitizing does not involve pre-attentive but also attentional processes in adults. Moreover, children with DD exhibit a subitizing deficit requiring them to count even small numerosities such as 2 and 3 (Moeller, Neuburger, et al., 2009). For symbolic numbers it was shown that perceptual encoding of a number (i.e., the time needed to read it) is influenced by its numerical magnitude (e.g., Brysbaert, 1995). Interestingly, the observed increase of reading times with number magnitude mirrored the word frequency effect known from word reading and thus seems to indicate a generalizable effect of familiarity on processing times irrespective of the cognitive domain.

With respect to a spatial representation of number magnitude, eye-tracking studies replicated and extended the evidence on attentional shifts to a peripheral region in space caused by the processing of number magnitude. This endorses the notion of an at least partially common representation for numbers and physical space as reflected in participants' eye-movements (e.g., Klein et al., 2014). Furthermore, the automaticity of this attentional shift indicates that number magnitude information is indeed activated whenever one encounters a number, even when it is irrelevant for the task at hand (e.g., Henik & Tzelgov, 1982). However, it also emphasizes the influence of more or less abstract cognitive concepts such as numbers on physical (eye-)movements (e.g., Fischer et al., 2004).

Regarding structural characteristics of external numerical representations, eye-tracking data suggest that multi-symbol number (including positive and negative multi-digit integers but also decimal numbers) are processed along the same underlying mechanisms in a decomposed parallel fashion (e.g., Huber, Cornelsen, et al., 2014). For more complex processes such as mental arithmetic eye-tracking allowed for differentiating processing stages involved in applying the carry operation in addition (e.g., Moeller et al., 2011b). More specific evaluation of participants' eye-fixation behavior even allowed for distinguishing between early bottom-up processing of magnitude information and later top-down processes indicating the application of rules in mental arithmetic. Nevertheless, these two processing schemes may interact (e.g., Moeller et al., 2011b).

Finally, as concerns influences of executive control on number processing, eye-tracking revealed how participants adapt their processing strategy in multi-symbol number processing to the experimental context by focusing on decision-relevant stimulus features (e.g., Huber, Mann, et al., 2014). Additionally, eye-tracking allowed for a more specific investigation of strategies which children as well as adults use to solve specific numerical tasks. With respect to the number line estimation task, eye-tracking provided independent evidence suggesting a crucial role of proportion judgments – and not numerical estimation – in solving this task. Finally, Heine et al. (2010) observed that developmental changes in numerical tasks such as number line estimation were reflected implicitly in children's eye-fixation behavior even before they manifested themselves in children's explicit responses.

In sum, this clearly indicates the added value of considering participants' eye-fixation behavior in numerical cognition research to gain deeper insights into the cognitive mechanisms underlying the processing of numerical information. However, evaluating the eye-tracking measures considered in the reviewed studies revealed that most studies focused on rather global measures such as the overall number of fixations or TRT on specific aspects of the stimuli. Importantly, there are only very few studies exploiting the possibilities offered by the eye-tracking methodology to differentiate between the underlying cognitive processes in a more fine-grained manner. In contrast to research on numerical cognition, this has been standard in reading research for decades. For instance, since the 1980s it has been common sense that measures such as first fixation and gaze duration on a stimulus are interpreted to reflect early stimulus-driven processes, whereas the overall number of fixations and TRT on the same stimulus are sensitive to later top-down influences such as plausibility judgments (e.g., Inhoff, 1984, 1985; Calvo & Meseguer, 2002; Deutsch et al., 2003; Joseph et al., 2008). Based on this differentiation highly sophisticated models of eye-movements in reading have been developed, which allow for very precise predictions on the locations and durations of eye-fixations in reading (e.g., E-Z Reader by Reichle, Rayner, & Pollatsek, 2003; SWIFT by Engbert, Nuthmann, Richter, & Kliegl, 2005). For the case of numerical cognition research, it needs to be said that only a small part of the reviewed studies made use of this opportunity to specify processing stages in number processing (e.g. Moeller, Fischer, et al., 2009a; Moeller et al., 2011b). Based on this preliminary evidence, we developed a model aimed at capturing the ongoing processes in number processing.

A model on the temporal dynamics of number processing

In the following, we aim at integrating above findings in a processing model of eye-fixation behavior in numerical cognition by adapting the model by Moeller, Fischer, et al. (2009a) covering the number bisection task. Importantly, comparable to the model of Moeller, Fischer, et al. (2009a), the current model is an adapted version of an early reading model by Just and Carpenter (1980). This model discerned early and late processing stages in early reading research and thus reflects the state-of-the-art in eye-tracking research on numerical cognition up to now. Against this background, we aimed at developing a model of the temporal dynamics of number processing based on eye-tracking studies in numerical cognition research from the last 40 years.

Considering the differentiation between early and later processing stages to be reflected in eye-movement measures (see above, e.g., Calvo & Meseguer, 2002), the present model also distinguishes an early stage of stimulus-driven bottom-up processing from later more top-down controlled ones. In line with evidence from reading research, we assume that during the early processing stage single numbers are identified and assigned their semantic and lexical values, whereas the later processing stages involve the integration of single numbers to provide a comprehensive representation of, for instance, the arithmetic problem at hand (see Fig. 1). Such integration processes are particularly relevant, when procedural rules (i.e., a carry operation in addition) need to be applied.

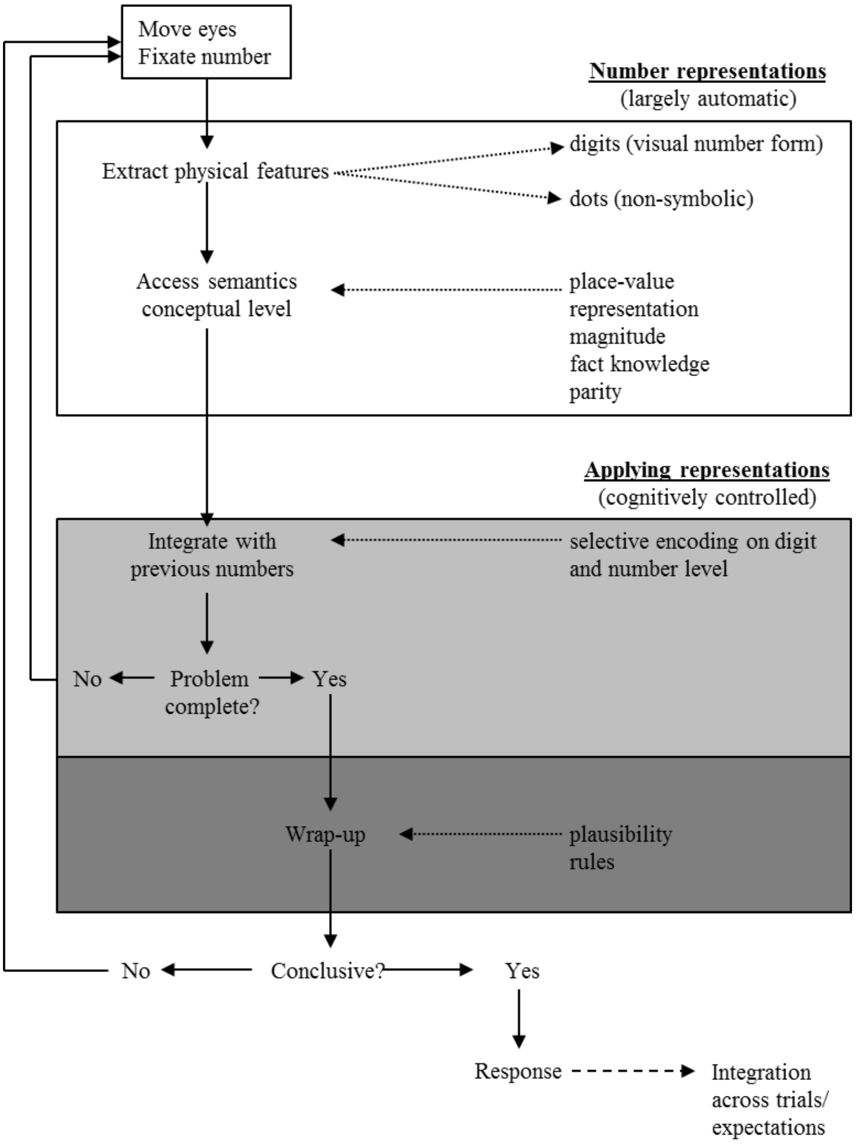

Figure 9.2: Model of the temporal dynamics of number processing based on eye-tracking data in numerical cognition. The full line boxes represent different processing stages. On the left side, the processing steps are depicted whereas on the right side numerical information actually processed at the respective processing stages is specified. The white box describes an early processing stage at which conceptual numerical representations are accessed largely automatic. Later processing stages are displayed in the light and dark grey box. Here, previously assigned numerical representations are integrated in the context of the task (light grey box) and later on an evaluation of plausibility and/or rule meaning takes place which is assumed to be under cognitive control (dark grey box).

Model description

In Figure 9.2, the upper white box indicates the initial stage of stimulus-driven bottom-up processing. At this stage, processing of numerical stimuli begins by extracting physical features of the respective stimuli that code numerical information – being it the numerosity of non-symbolic objects or symbolic digits[15]. For non-symbolic magnitudes, Burr and Ross (2008; see also Ross & Burr, 2010) claimed that a number is a primary sensory attribute, which is perceived directly. In line with this, Harvey, Klein, Petridou, and Dumoulin (2013) observed neural populations in the parietal cortex to be organized topographically forming a numerosity map (but see Gebuis, Gevers, & Cohen Kadosh, 2014). As to symbolic numbers, their recognition sets the stage for the access to the semantic and lexical numerical representations of the stimuli. Most importantly, the magnitude information of the respective digits is activated at this stage. In case of multi-digit numbers the respective digits are integrated into the place-value structure of the Arabic number system to represent the overall magnitude. Furthermore, specific semantic attributes such as fact knowledge about a number being the product of two other numbers (e.g., Galfano, Rusconi, & Umiltà, 2003) or other associated labels (i.e., 747 representing a type of airplane, cf. Alameda, Cuetos, & Brysbaert, 2003) are assigned. All this is assumed to happen in a stimulus-driven and largely automatic manner (e.g., Henik & Tzelgov, 1982). This captures the eye-tracking evidence of pre-attentive and attentive processes in subitizing (Sophian & Crosby, 2008), and the finding that – comparable to effects of word frequency in reading – gaze durations in number reading increase with the magnitude of the number read (e.g., Brysbaert, 1995). Additionally, all the processes involved in these actions occur on the level of an individual (multi-digit) number. Hence, the processed number is not yet set into relation with other numbers at this stage.

In our model, we assume a first integration (i.e., putting into relation) with previously processed numbers of the same trial or problem to occur on an intermediate processing stage (depicted as light grey box in Figure 9.2). Here, selective encoding of digits within numbers as well as across numbers takes place. This process is reflected by the number of fixations in an interest area as well as the fixation location. Particularly in magnitude comparison tasks a selective encoding within numbers can be observed. Moeller and colleagues (2009b) showed that in a two-digit number comparison task, the unit digits are fixated more often than the decade digits. This selective encoding is likewise the case in decimal fractions and multi-symbol numbers (e.g., Huber, Cornelsen, et al., 2014; Huber, Klein, et al., 2014). Thus, for solving a magnitude comparison task,

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[15] Please note that there is an ongoing debate on whether symbolic and non-symbolic presentation formats address the same underlying representation of numbers or not (e.g., Cohen Kadosh & Walsh, 2009 for an overview and discussion). However, this is beyond the scope of this article.

not all digits are fixated equally often. Rather, selective encoding takes place when integrating the respective number with previously processed numbers. Further evidence for such an early integrative processing stage results from the observation that the multiplicative relatedness of two numbers (i.e., 24_28) is reflected in increased gaze duration on the second number (e.g., Moeller, Fischer, et al., 2009a). This indicates that, when fixating the second number, multiplicative relatedness needs to be processed in addition to the magnitude of the respective number which in turn increases gaze duration on this number compared to the previous one. This idea of an integrative processing of subsequent numbers is further supported by eye-fixation data from mental addition. Moeller et al. (2011b) found that even first fixations on the unit digit of the second summand increased with the sum of the unit digits of both summands. Thus, first fixation durations increased with the summed value of two digits reflecting an integration of information across numbers quite early in processing. However, it is important to note that these early integrative processes seem to be limited to an integration of semantic attributes assigned in the first processing stage and thus assigned to the individual (multi-digit) numbers (i.e., magnitude, or being part of a multiplication table).

On the other hand, during integration processes specific procedural rules, solution strategies or plausibility judgements are applied. These rules which require at least preliminary knowledge of the whole problem are restricted to a final wrap-up stage (depicted as dark grey box in Figure 9.2). Effects occurring at this stage usually affect measures of late processing such as TRT or the overall number of fixations or even refixations of specific parts of a stimulus. This proposition is backed by eye-tracking data from the number bisection task. For this task Moeller, Fischer, et al. (2009a) observed that whether a number triplet was bisectable by an integer mean or not (i.e., 23_25_29 vs. 23_25_28, respectively) reliably influenced total reading times but had no influence on gaze durations. As bisection possibility can be inferred from the parity status of the two outer numbers (i.e., only when both outer numbers are of the same parity there is an integer mean of the triplet) all three numbers need to be processed before this plausibility check can be performed. In line with this, Moeller et al. (2011b) observed that the need for a carry operation specifically increased TRT on and refixations of the unit digits. The carry operation as a procedural rule can only be applied after the initial integration has been completed (i.e., sum of the unit digits of the summands is equal to or larger than 10). Thus, the actual application of this rule influences TRT which further substantiates the idea of a final wrap-up stage involving the application of more complex syntactic rules.

Taken together, the stage of early integration with previously processed numbers (see the light grey box in Figure 9.2) and the subsequent wrap-up stage (see the dark grey box in Figure 9.2) reflect later integrative stages of number processing. Here, number representations are not only assigned, but stored in working memory and applied with increasing cognitive control over this application process, the later the processing step. Moreover, the transition between the two stages may be fluent and task-dependent. However, to differentiate between early and late processing, a certain task-complexity is needed since later processing stages require some kind of procedural rules, plausibility checks, etc., which leads to more efficient processing when applied.

After a sufficiently conclusive solution has been identified in the wrap-up stage, a response is given. Importantly, it should be noted that participants not only adapt their processing styles and strategies within one trial but also across trials. For instance Loetscher et al. (2010) found that whether the next number to be processed will be smaller or larger than the actually produced one in a random number generation task is indicated by participants' eye-movements. As suggested by Rinaldi et al. (2015), participants may create a representation of the necessary number range in working memory and refer to this representation during the task. However, there is also the case that responses on earlier trials influence subsequent trials by raising expectations about what is next. Huber, Moeller, and colleagues (2014) and Huber, Mann, and colleagues (2014) showed that this not only led to differing response patterns in terms of reaction times but also differences in participants' eye-fixation patterns. In particular, the location of the first fixation was adapted to fixate the decision-relevant parts of the stimuli as early as possible.

Developmental aspects

Although mainly based on data from adults, some assumptions on developmental aspects of the model will be discussed in the following. First of all, it is important to note that children are well "equipped with the basic oculomotor abilities to maintain fixations and to plan and execute saccades to selected targets" (Feng, Miller, Shu, & Zhang, 2009, p. 732). Additionally, there is accumulating evidence suggesting that children (from about the age they enter primary school) do not differ from adults in their oculomotor abilities regarding the accuracy of saccades to a given target (e.g., Salman et al., 2006), the distribution of landing positions within a word when reading (e.g., Joseph, Liversedge, Blythe, White, & Rayner, 2009), as well as the ability to extract visual information during fixation (e.g., Blythe, Liversedge, Joseph, White, & Rayner, 2009; see McConkie et al., 1991 for a review on children's eye-movements). Thus, any differences in children's fixation behavior should not result from insufficient oculomotor abilities (see also Moeller et al., 2011a).

With respect to the current model we propose that the distinct processing stages need to develop over time. That is, at the initial level of automatic processing (i.e., extracting physical features, assigning semantic attributes) children first have to attribute symbols to their specific numerical meaning. The learning of such number semantics might be driven by external characteristics of numbers such as their frequencies similar to early word learning in infants (e.g., Saffran, Aslin, & Newport, 1996). Accordingly, effects related to the number specific characteristics at this processing stage (e.g., frequency effects, Brysbaert, 1995) should only occur after children master the assignment of the respective semantic attributes to single digits and multi-digit numbers. In children with DD, this initial stage of number processing may already lack automation (e.g., Moeller, Neuburger, et al., 2009). Once number words, symbols and their meaning are stored in long term memory, the initial stage of this model is accessed and performed automatically whenever one sees or hears a number (Henik & Tzelgov, 1982). For later integrative stages that involve working memory (e.g., Rinaldi et al., 2015) and cognitive control (e.g., Huber, Cornelsen, et al., 2014; Moeller, Fischer, et al., 2009b) or the application of arithmetic rules (e.g., Moeller et al., 2011b) further experience with the manipulation of numbers is required (Moeller et al., 2011a). As a consequence, it should be possible to observe how the prototypical eye-fixation patterns in, for instance, addition, develop over time by investigating children of different ages. In line with the initial results of Moeller et al. (2011b) the fixation pattern should develop from more or less unspecific to very specific distributions of fixations reflecting processing steps and difficulties. Importantly, this development might co-occur with the maturation and specification of neural networks for number processing in the children's brains. Over developmental time a shift from a strong involvement of frontal areas associated with domain-general processes of attention and working memory to an increasing engagement of intraparietal and posterior parietal regions in symbolic number processing (e.g., Ansari, Garcia, Lucas, Hamon, & Dhital, 2005; Ansari, 2008) and mental arithmetic (e.g., Rivera, Reiss, Eckert, & Menon, 2005; see Kaufmann et al., 2011 for a review and meta-analysis) takes place. Thus, the process from learning to automation by means of experience is likewise visible on a neural level.

9.9 Perspectives

The increasing number of eye-tracking studies in recent years emphasizes the relevance and the benefits of considering participants' eye-fixation behavior in numerical cognition research. However, compared to other domains such as reading, research in the domain of numerical cognition does not yet exploit both the tasks and the possibilities given by eye-tracking. Comparing research on number processing to reading research, one may assume that reading letters is equivalent to reading digits on a very basic, lexical level (although digits clearly carry more semantic content than letters). Further, processing words might correspond to processing multi-digit numbers on a more complex lexical and (morpho-)syntactic level since the digits of multi-digit numbers have to be integrated into the place-value system (Dehaene & Cohen, 1995). Additionally, reading sentences might be comparable to reading and solving arithmetic equations since both underlie rule-governed hierarchies, and, thus, syntax. While reading research has a long time ago reached the investigation of sentences using eye-tracking (e.g., Traxler et al., 1996; see Clifton et al., 2007 for a review), research on its numerical/arithmetic equivalent is still in its beginning. Thus, to catch up with reading research, more complex tasks consisting of rule-governed structures may be of interest. Based on such numerical syntax, a more abstract level of the description of number processing compared to the description of a formal language can be achieved. Moreover, by investigating more complex, rule-governed structures, the possibilities offered by the eye-tracking methodology may be exploited more comprehensively. Scan paths which combine the study of fixation position and duration as well as saccade duration, thus reflecting the precise time course of processing, may be considered for a deeper understanding of the underlying processes involved in processing numerical syntax (e.g., Noton & Stark, 1971; Zangemeister, Shermant, & Stark, 1995). So far, the use of these measures has not been established in numerical cognition research yet, even though it displays a valuable source of information. Thus, future research is needed to take the evaluation of participants' eye-fixation behavior in numerical cognition research to the state-of-the-art in reading research. On the other hand, procedures, measures, and analyzes from reading research are a source of inspiration for future investigations in numerical cognition research. The increasing number of eye-tracking data in numerical cognition shows that we are on a promising track.

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Part III: Discussion

General discussion

The aim of the present thesis is to evaluate domain-specific and domain-general contributions to number processing by focusing on two major goals: specifying the assumptions the TCM makes about domain-specific numerical and domain-general parietal processes involved in number processing as revealed by neurofunctional and behavioral data in Section 1 (principally independent from temporal aspects and time-critical methods) and extending the scope of the TCM by enriching the model with early bottom-up and later top-down mediated processing stages as revealed by eye-tracking data in Section 2 (based on findings of time-critical methods).

The general discussion is organized in three major parts: First, the major results of the empirical studies are discussed with respect to the research questions of the present thesis. Second, an extension of the TCM based on the empirical findings is proposed and discussed aiming at integrating temporal aspects occurring early and late while processing numbers with neurofunctional correlates. The assumptions of this extension will be briefly evaluated by means of neuropsychological data and developmental aspects. Third, possible perspectives for future research are presented that might help to validate the proposed model extension and to further clarify aspects of temporal dynamics and neural underpinnings of numerical cognition.

10 Discussion of the empirical findings

In the following I will briefly summarize the main findings of the empirical studies presented in this thesis.

10.1 Section 1: Domain-specific numerical and domain-general parietal number processing

The main focus and the major contribution of the TCM is the assignment of domain-specific structure-function-relationships. Domain-general processes were assumed to be represented in frontal brain regions in the TCM. Yet, besides domain-specific numerical processing the parietal cortex is also involved in sensory, motor, and different cognitive functions (Culham & Kanwisher, 2001; Humphreys & Lambon Ralph, 2015, 2017). In the present thesis, some assumptions the TCM makes for the parietal cortex were addressed in Section 1, in which domain-specific numerical as well as domain-general parietal mechanisms involved in number processing were evaluated. In three studies, I aimed at specifying functions the TCM proposed for the parietal cortex.

In Study 1, I investigated whether symbolic and non-symbolic proportions share a neural correlate for relative magnitude processing comparable to absolute magnitude processing in the analogue magnitude code of the TCM.

The aim of Study 2 was to extend the assumptions of the TCM for intraparietal brain areas by examining domain-general processes related to, but beyond overall magnitude processing in proportion processing and whether these processing mechanisms share one underlying neural process. In this study, I also examined the neural mechanisms involved in processing bipartite part-whole relations reflecting integration of numerical information.

Finally, in Study 3, I investigated how automatically distinct aspects of multi-symbol numbers (e.g., magnitude, polarity signs, place-value structure) are associated with space in children who were just introduced to this numerical concept.

10.1.1 Findings of Study 1: Processing relative magnitude information

As regards the processing of relative magnitude information, Study 1 suggested that the notion of the TCM regarding an abstract and notation-independent analogue magnitude code for absolute magnitude in bilateral IPS (Dehaene & Cohen, 1995, 1997; Dehaene et al., 2003) can be extended to relative magnitude information (Jacob, Vallentin, & Nieder, 2012; Lewis, Matthews, & Hubbard, 2016; Matthews, Lewis, & Hubbard, 2016). Furthermore, the results indicated an occipito-parietal network to be involved in relative magnitude processing. The IPS seems to be involved specifically in the processing of relative magnitude information comparable to activation found for the processing of absolute magnitude (Piazza et al., 2004, 2007; Pinel et al., 2001). Yet, activation found for relative magnitude processing seems to be more pronounced in right IPS. Moreover, activation observed in occipital areas might reflect higher order visual processing as well as decoding of the visual form as a precursor of the processing of semantic features (Ansari, 2008; Fias, Menon, & Szucs, 2013; Jolles et al., 2016; Dotan & Friedmann, 2017). Thus, magnitude processing of proportions (e.g., fractions, decimals, dot patterns, and pie charts) as indicated by the neural instantiation of the numerical distance seems to rely on similar neural correlates as compared to processing absolute magnitude. Hence, the assumptions for the analogue magnitude code as proposed by the TCM can be extended to the processing of relative magnitude information. Moreover, activation in bilateral superior, inferior and right middle occipital gyrus seems to reflect higher order visual processing. Importantly, via the dorsal visual stream these brain areas interact with the IPS for the semantic representation of magnitude and quantity (Menon, 2015).

10.1.2 Findings of Study 2: Numerical processing beyond magnitude

Although it was shown that single neurons in intraparietal regions in macaques respond differently to distinct numbers of items (Nieder et al., 2006; Roitman et al., 2007), bilateral IPS is not only associated with domain-specific numerical processing. Rather, bilateral IPS is also involved in a variety of domain-general processes as part of the higher order association cortex, (Critchley, 1953;

Culham & Kanwisher, 2001). Thus, the IPS is also associated with domain-general cognitive functions beyond magnitude processing such as top-down control, working memory, and goal-directed processes besides domain-specific numerical processes (Cabeza, 2008; Humphreys & Lambon Ralph, 2015, 2017). Nevertheless, these domain-general parietal processes might play an important role during magnitude processing.

As regards this issue, Study 2 of the present thesis revealed shared activation in the bilateral inferior parietal lobule (IPL) for the processing of symbolic and non-symbolic proportions related to, but beyond magnitude processing. This is in line with a recent meta-analysis by Sokolowski and colleagues (2017) showing joint activation for processing symbolic and non-symbolic natural numbers in this specific brain region. The present results further extend these findings as we showed joint activation for symbolic and non-symbolic proportions instead of integers and numerosities. This indicates that bilateral IPL seems to be crucially involved in number processing in general. Yet, when conducting complementary analyses on the very same data set (Study 1), we found joint activation for the specific processing of magnitude information primarily in right IPS. Thus, the core area for relative magnitude processing (as reflected by the numerical distance) differed from the brain areas found in Study 2, as this activation was found to be more anterior and bilateral. Hence, the shared activation for proportion processing found in bilateral IPL related to, but beyond overall proportion magnitude processing, might rather reflect shared task demands. This might include processes of visuo-spatial and top-down attention (Humphreys & Lambon Ralph, 2015, 2017), estimation, summation, and calculation (Castelli, Glaser, & Butterworth, 2006; Holloway, Price, & Ansari, 2010; Venkatraman, Ansari, & Chee, 2005), working memory during maintenance and manipulation of the stimuli (Humphreys & Lambon Ralph, 2015; Jonides et al., 1998), or response-selection (Göbel et al., 2004).

Taken together, these assumptions are also in line with the notion of a domain-general executive system in parietal cortex for shared non-automatic top-down mediated processes (Humphreys & Lambon Ralph, 2015, 2017). The interaction of this domain-general executive system and smaller domain-specific subregions as shown by Study 1 (e.g., for the processing of number magnitude information) might enable the adequate processing of proportions.

The conjunction analysis of Study 2 revealed a shared neural correlate for proportion processing related to, but beyond magnitude processing, although the stimuli (i.e., fractions, dot patterns, pie charts, and decimals) were conceptually distinct (part-whole vs. base-10): whereas the magnitude of decimals is reflected directly based on their base-10 structure similar to the magnitude of a multi-digit number (by skipping the leading 0), the two parts of a bipartite part-whole proportion have to be integrated and put into relation (e.g., denominator and numerator for fractions). Yet, a shared neural correlate does not necessarily indicate a shared underlying neural process (Cohen

Kadosh et al., 2005; Pinel et al., 2004). Therefore, we additionally conducted an RSA in the activated clusters of the bilateral IPL to evaluate the activation patterns of the different presentation formats in a more fine-grained way. In fact, the RSA revealed different activation patterns for decimals and part-whole relations, respectively. Thus, fractions, dot patterns, and pie charts seemed to share an underlying neural process while the neural processing of decimals differs from the other formats. This might result from the differing underlying structure of these proportions: while decimals directly reflect number magnitudes in a base-10 notation, fractions, dot patterns, and pie charts consist of bipartite part-whole structures and require additional processing of proportional aspects like integration and putting into relation of the two components. Thus, depending on the structure of the proportion the task demands might differ resulting in distinct activation patterns (Humphreys & Lambon Ralph, 2015; see also Hugdahl, Raichle, Mitra, & Specht, 2015).

To take a closer look at the neural correlates of part-whole relations reflecting the integration of numerical information, we additionally compared part-whole proportions (i.e., fractions, dot patterns, pie charts) to decimals. We found a widespread network including activation in bilateral IPL extending to occipital gyrus, bilateral SMA, bilateral insula, and bilateral middle and inferior frontal gyrus. Activations found in parietal cortex covered both the clusters found for magnitude-specific processing in Study 1 and clusters associated with rather domain-general top-down processing reflecting spatial attention, working memory, and other executive functions found in the conjunction analysis of Study 2 (Fias et al., 2013; Humphreys & Lambon Ralph, 2017). Co-activation in bilateral middle and inferior frontal areas further substantiated the idea of domain-general processes involved because these brain regions were associated with visual working memory (Song & Jiang, 2006), higher cognitive monitoring and manipulation of information (Christoff, John, & Gabriel, 2000; Ranganath, Johnson, & D'Esposito, 2003), as well as strategy choice and planning (Arsalidou & Taylor, 2011; Dehaene & Cohen, 1997).

Importantly, the areas found for part-whole processing correspond to a so-called multiple demand system (MD; Duncan, 2010; Fedorenko, Duncan, & Kanwisher, 2013) or an extrinsic mode network (EMN; Hugdahl et al., 2015) reflecting diverse cognitive and executive control demands such as focused attention, goal maintenance, strategy selection, working memory, and performance monitoring (Fedorenko et al., 2013; Hugdahl et al., 2015). This further corroborates the assumption of domain-general processes involved in proportion processing within the human brain including parietal areas. Thus, Study 1 and 2 together indicate that processing proportions is accomplished by the complex interplay of domain-specific brain areas like parts of the IPS as reflected by Study 1 and domain-general cognitive and neural mechanisms as indicated by Study 2 (Duncan, 2010; Fedorenko et al., 2013; Hugdahl et al., 2015).

10.1.3 Findings of Study 3: Automatic association of numbers and space

Another interrelation between domain-specific and domain-general processes is reflected by associations of numbers and space. The analogue magnitude code of the TCM is described as a spatial map of magnitude or number line (Dehaene et al., 2003). On the neural level, this association can be observed in activation of brain regions associated with spatial attention when processing number or mental arithmetic tasks (Knops, Thirion, Hubbard, Michel, & Dehaene, 2009a; Simon et al., 2002). On the behavioral level, one of the most prominent examples for SNAs is the SNARC-effect: small numbers are associated with the left and large numbers with the right side in space (at least in Western cultures), even if number magnitude is not relevant for the task at hand (e.g., in parity judgment tasks; Dehaene, Bossini, & Giraux, 1993; Wood, Willmes, Nuerk, & Fischer, 2008). Thus, number magnitude seems to be automatically associated with space (but see van Dijck & Fias, 2011). Yet, there are studies showing that SNAs strengthen with increasing age and experience reflecting a development towards an automatic association between numbers and space (Ninaus et al., 2017). The results of Study 3 support the latter assumption. In 6th graders who were just introduced to the numerical concept of multi-symbol numbers, we only found a significant digit-direction congruency effect (cf. SNARC), but neither a sign-direction congruency (cf. OSSA; Pinhas, Shaki, & Fischer, 2014) nor a sign-digit-compatibility effect (Huber, Cornelsen, et al., 2014). The respective null effects were further substantiated by Bayesian analyses. Thus, associations of numerical concepts with space seem to take longer to develop with increasing complexity of the concept.

For the case of multi-symbol numbers, this might involve aspects of embodied cognition (e.g., Barsalou, 2008; Fischer, 2012). These theories propose that abstract representations such as number magnitude might be rooted in bodily and physically perceivable interactions and experiences with the environment (e.g., Domahs, Moeller, Huber, Willmes, & Nuerk, 2010; Moeller et al., 2012). For natural numbers, an embodied representation is possible as these numbers and operations on these numbers (e.g., addition or subtraction) can be physically perceived (e.g., having three apples and eating two of them). Hence, these numbers and operations can be grounded and bound to physical experience (Domahs et al., 2010). However, an embodied representation does not exist for negative numbers (e.g., one cannot have -4 apples). For this reason, this numerical concept might not be grounded in nature, but rather reflects an abstract mathematical concept. As a result, the association with space seems to take longer and develop only with increasing experience with this complex numerical concept.

Taken together, the findings of Section 1 suggest that i) comparable to absolute magnitude, relative magnitude information is processed notation-independently in intraparietal brain areas, ii) number processing related to, but beyond magnitude is associated with activation in bilateral IPL indicating domain-general processes to be represented in this specific brain region, and iii) associations between numbers and space develop only with increasing experience for complex numerical concepts. Thus, the parietal cortex is involved in both domain-specific numerical as well as domain-general processes. However, the association between numbers and space seems to be dependent on experience.

10.2 Section 2: The temporal dynamics of number processing

The number of studies on the temporal dynamics of number processing using time-critical neuro-cognitive methods increased in recent years emphasizing the relevance of investigating both the spatial as well as the temporal resolution of processes involved in number processing (e.g., Dehaene, 1996; Kiefer & Dehaene, 1997; Teichmann et al., 2018; Pinheiro-Chagas et al., 2018). Eye-tracking provides a complementary approach to capture and account for the temporal dynamics of cognitive processes. Reading research showed that a distinction between early and later processing steps can be achieved by means of different eye-tracking measures (Calvo & Meseguer, 2002; Joseph et al., 2008; Just & Carpenter, 1980). For this reason, Study 4 of the present thesis focused on and discussed empirical eye-tracking studies of the last 40 years from the domain of numerical cognition with the aim of differentiating underlying cognitive processes in numerical cognition into early stimulus-driven mechanisms and later cognitively controlled and top-down mediated processes. To pursue this issue, measures indicating temporal sequences in cognitive processes as revealed by reading research were used to distinguish between early and late processing steps in numerical cognition: while first fixation duration and gaze duration are sensitive to early stimulus-driven processes, overall number of fixations, total reading times, and refixations rather indicate later top-down mediated processes. Based on this differentiation, a model on the temporal dynamics of number processing was postulated in Study 4 by adapting a model by Moeller and colleagues (2009b) covering the number bisection task. Importantly, comparable to the model of Moeller et al. (2009b), the current model is an adapted version of an early reading model by Just and Carpenter (1980) describing early largely automatic and later cognitively controlled processes.

The model of Study 4 distinguishes between an early stage of stimulus-driven bottom-up processing and later top-down controlled ones by means of eye-tracking measures (see above, e.g., Calvo & Meseguer, 2002). In line with evidence from reading research, I assume that, after extracting the visual features of the stimuli, individual (single- or multi-digit) numbers are identified and assigned their semantic and lexical values (e.g., magnitude, place-value structure, parity, fact knowledge) at the conceptual level of the early processing stage, whereas the later processing stage involves the integration of these individual numbers to provide a comprehensive representation of, for instance, the arithmetic problem at hand. Such integration processes are particularly relevant, when procedural rules (i.e., a carry operation in addition) need to be applied.

11 Integrating temporal and neuro-functional processes involved in numerical cognition

In the following, I aim at proposing a first attempt of a model extension for the TCM by integrating the assumptions of the TCM with my findings from Studies 1 to 4 and specifying both aspects of the temporal dynamics and neural processes involved in number processing. To pursue this issue, the current model extension of the TCM will be described in detail based on three distinct processing stages as proposed by eye-tracking data. The three processing stages are divided into a first visual input stage, a second early, largely automatic and stimulus-driven conceptual stage, and a third processing stage including later top-down and cognitively controlled processes. In the next step, the corresponding neural correlates are assigned to these three processing stages, resulting in the Three Stages Account (TSA) of visual number processing (see Figure 11.1).

The starting point of this model extension is the eye-tracking model proposed in Study 4 of the present thesis (cf. p. 174), which gives an overview of aspects of the temporal dynamics of number processing as revealed by eye-tracking studies of the last 40 years proposing three processing stages (i.e., visual input, early conceptual processes, and late processes). As the model is based on eye-tracking data, it is important to note here that the evaluated processes are based on visual inputs. Thus, the resulting model extension of the TCM aims at describing aspects of temporal dynamics and neural processes involved in visual number processing. The question whether parts of this model also apply to other modalities is beyond the scope of the present thesis.

The TSA is structured as follows: with slight modifications compared to the model proposed in Study 4, the temporal dynamics depicted on the left distinguish a visual input stage (see orange box in Figure 11.1) from an early stage of largely automatic stimulus-driven bottom-up processes (see blue box in Figure 11.1) and a later cognitively controlled and top-down mediated processing stage (see green box in Figure 11.1).

At the visual input stage, physical features of the stimuli are extracted whereas semantic and lexical values are assigned on the conceptual level at the early processing stage. At the later processing stage, numbers are integrated to provide a comprehensive representation of the numerical task at hand before procedural rules are applied and, finally, a response is given.

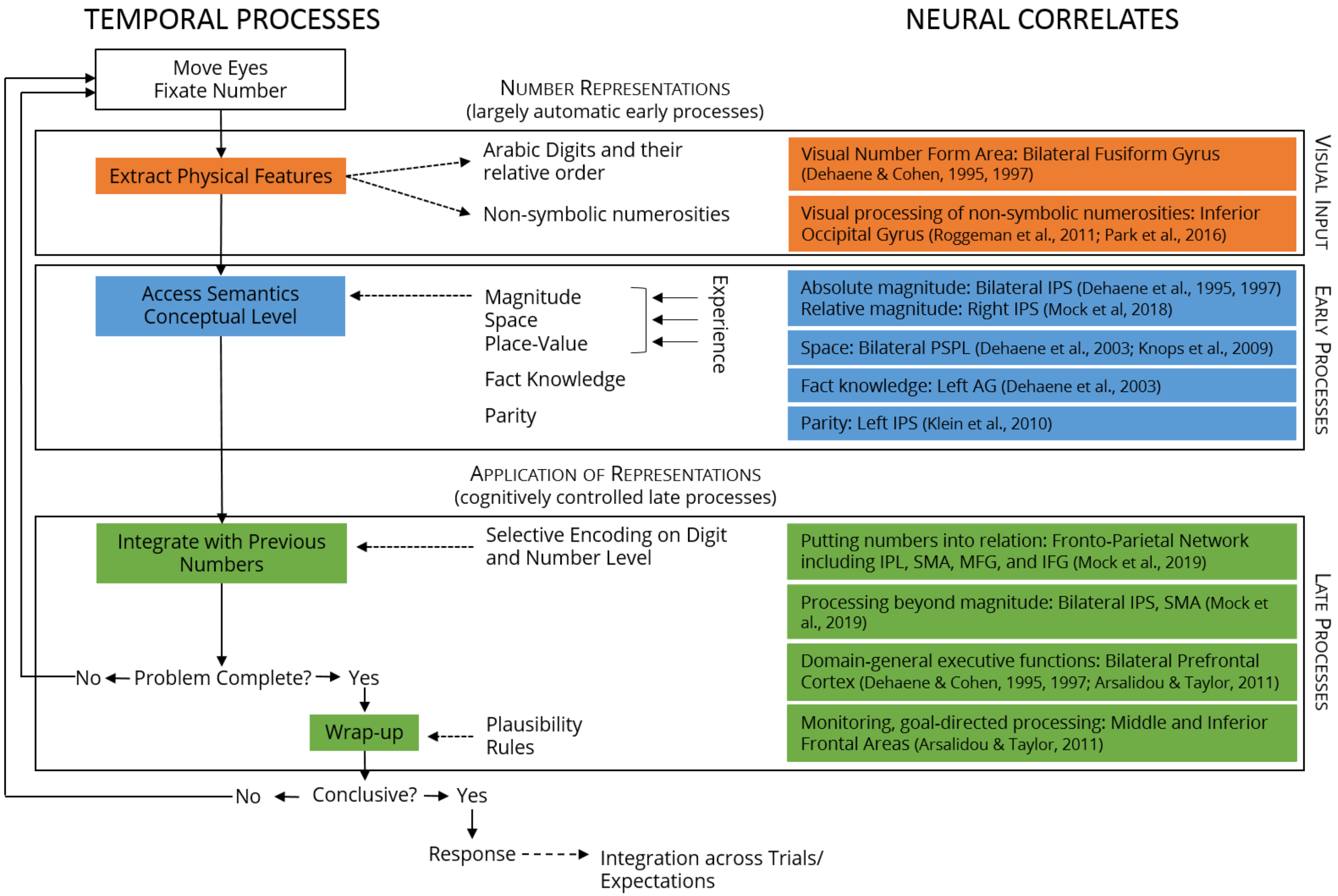

Figure 11.1: Three Stages Account (TSA) of visual number processing. On the left side, the temporal sequences are depicted as revealed by eye-tracking studies. In the middle, (numerical) representations are assigned to the respective temporal processing stage. On the right side, the associated neural correlates of the respective representation are presented. The orange box displays the visual input processing stage, while the blue box depicts early stimulus-driven and largely automatic processes on the conceptual level in which semantic information is accessed. The green box represents later rather top-down and cognitively controlled higher order processes in which context integration and evaluations of plausibility and/or rules take place.

Each of these stages is again split into three columns. The left column indicates the temporal sequences during number processing as revealed by eye-tracking data on numerical cognition of the last 40 years (cf. Study 4). The middle column represents the corresponding number representations (orange and blue box) or the application of those representations (green box). Finally, in the right column the neural correlates of the specific processes are mapped onto the corresponding temporal processing stage.

It should be emphasized that TSA provides only a tentative account based on the synthesis of the present findings and the existing literature so that it requires further validation by direct experimentation. Nevertheless, TSA is a first step towards a more comprehensive description of the complex processes underlying numerical cognition by integrating both aspects of temporal dynamics and the corresponding neural correlates.

11.1 Extension of the TCM: implementing the Three Stages Account (TSA)

In the following, the processes involved in the TSA will be explained in more detail. At each processing stage, the sensory or cognitive processes involved, as revealed by eye-tracking data, will first be described before they will be mapped onto their corresponding neural correlates as revealed by neuro-functional data based on the present findings and the existing literature. Step by step, the TSA will be implemented and integrated according to the proposed three stages extending the TCM and its specifications (Arsalidou & Taylor, 2011; Dehaene et al., 2003; Klein et al., 2016). Furthermore, the neural interrelations between the involved brain areas will be discussed in order to evaluate the assumptions of the TSA based on the existing literature and the present findings.

11.1.1 Stage 1: Visual input processing

At the first stage visual input is processed. The upper orange box indicates the initial stage of stimulus-driven bottom-up sensory processing (see Figure 11.1). At this stage, physical visual features of the respective stimuli that code numerical information (e.g., Arabic numbers or non-symbolic numerosities[16]) are extracted. Within visual processing, Dotan and Friedmann (2017) assume different processes to be involved. First, the decimal structure of a number is extracted at this processing stage including the detection of 0's and their positions, number length, and parsing large multi-digit numbers into triplets (e.g., 65,432). In a second step, this information is sent to the encoders of digit identity and order (Dotan & Friedmann, 2017). Importantly, Dotan and Friedmann

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[16] Please note that there is an ongoing debate on whether symbolic and non-symbolic presentation formats address the same underlying representation of numbers or not (e.g., Cohen Kadosh & Walsh, 2009 for an overview and discussion).

(2017) do not suggest that the place-value structure or the absolute positions of the digits of the respective number are encoded at the visual processing stage, but rather their relative order. This relative order of the digits in the string is encoded at this early processing stage so that semantic information can succeed at the next processing stage.

On the neural level, visual processing of numbers is associated with activation in the visual number form area (VNF) in bilateral fusiform gyrus (Dehaene & Cohen, 1997) and inferior temporal gyrus for symbolic numbers (Daitch et al., 2016; Grotheer, Ambrus, & Kovács, 2016; Grotheer, Herrmann, & Kovács, 2016; Shum et al., 2013). The causal involvement of inferior temporal cortex in early visual number processing was recently demonstrated by a transcranial magnetic stimulation (TMS) study. The detection of briefly presented Arabic numbers was significantly impaired when TMS was targeted at this specific brain area (Grotheer, Ambrus, & Kovács, 2016).

The initial visual processing of non-symbolic numerosities is assumed to be subserved by inferior occipital gyrus (IOG; Park, Dewind, Woldorff, & Brannon, 2016; Roggeman, Santens, Fias, & Verguts, 2011). Interestingly, the more structured the presented numerosities (e.g., structured in dice patterns), the more likely they are processed in the more anterior VNF as indicated by the dashed arrow in Figure 11.2 (Bloechle et al., 2018).

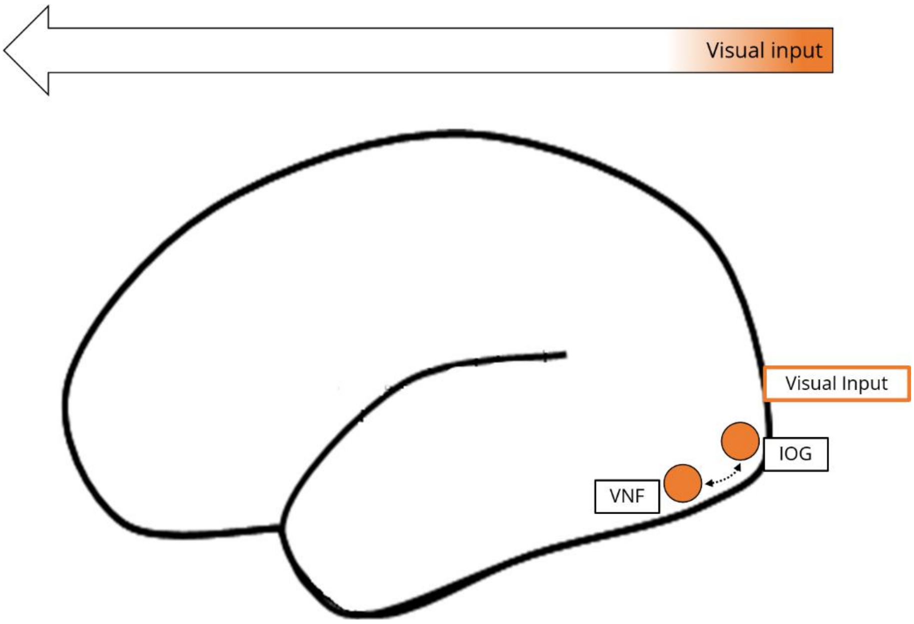

Figure 11.2: Neural correlates of the first processing stage, visual input processing of the TSA. Physical features and relative order of symbolic digits are extracted in VNF, while non-symbolic numerosities are initially processed in IOG. The more structured non-symbolic numerosities are, the more likely they are processed in VNF as indicated by the dashed arrow.

11.1.2 Stage 2: Largely automatic early processes on the conceptual level

After extracting the physical features of the respective stimuli, their semantics are accessed at the conceptual level at the next processing stage depicted in blue (see Figure 11.1). On the neural level, the connection between the visual input stage and early processes at the conceptual level follows the dorsal visual processing stream (Klein et al., 2016). It is assumed that the dorsal processing stream (also referred to as "where" stream) is involved in visual guidance of actions, spatial relations between visually perceived objects, sequence execution, and sensory-motor integration while the ventral visual processing stream (also referred to as "what" stream) is associated with object recognition and the relation and implementation of visual properties which are related to semantic meaning (e.g., Goodale & Milner, 1992; Rijntjes, Weiller, Bormann, & Musso, 2012).

At Stage 2 of the TSA, magnitude information of the extracted physical features making up the respective numbers is accessed and activated. Interestingly, magnitude for digits seems to be accessed earlier than for non-symbolic dice stimuli which might be due to faster conversions into an abstract representation for digits compared to less frequent dice stimuli (Teichmann et al., 2018). In case of multi-digit numbers, the relative order of the digits which was extracted at the early visual stage is integrated into the place-value structure of the Arabic number system to assign number semantics and to represent overall magnitude of the respective numbers. Using the place-value structure, a number word frame is created dependent on language-specific structures (e.g., in German and Arabic, the ones word precedes the tens word; Dotan & Friedmann, 2017). Furthermore, magnitude information is associated with space at this stage (Dehaene et al., 1993; Wood et al., 2008). Additionally, specific semantic attributes such as parity, fact knowledge about a number being a product of two other numbers (e.g., Galfano, Rusconi, & Umiltà, 2003) or other associated labels (i.e., 747 representing a type of airplane, cf. Alameda, Cuetos, & Brysbaert, 2003) are assigned. All this seems to happen in a stimulus-driven bottom-up and largely automatic manner (e.g., Henik & Tzelgov, 1982). This is reflected by eye-tracking evidence of pre-attentive and attentive processes in subitizing (Sophian & Crosby, 2008), and gaze durations in number reading which increase with the magnitude of the number read comparable to effects of word frequency in reading (e.g., Brysbaert, 1995). How automatically in particular number magnitude and place-value integration are associated with space depends, however, on experience with the respective number concept as Study 3 of the present thesis showed. Thus, the association with space develops only with increasing experience with a specific (number) concept (e.g., place-value integration, polarity signs, multi-symbol numbers; Study 3; Ninaus et al., 2017).

According to the TCM, absolute number magnitude is processed in bilateral IPS (Dehaene & Cohen, 1995, 1997; Dehaene et al., 2003). Importantly, in line with the assumptions of the TSA, recent findings suggest that the processing of magnitude information in parietal regions seems to occur in an automatic bottom-up way (Cohen Kadosh, Bien, & Sack, 2012; see Figure 11.3). Cohen Kadosh and colleagues (2012) used transcranial magnetic stimulation (TMS) to examine automatic magnitude processing in the parietal lobes by employing a size congruity effect. Here, participants compared two numerical stimuli according to their physical (not numerical) size. In congruent trials, the physically larger digit (here indicated in bold print) was also numerically larger (e.g., **6** vs. 3) whereas in incongruent trails the physically larger digit was numerically smaller (e.g., 6 vs. **3**). Even though irrelevant for the task at hand, numerical magnitude interfered with physical size, which indicates that numerical magnitude is processed automatically (Henik & Tzelgov, 1982; Cohen Kadosh et al., 2012). This automatic processing was disrupted following stimulation over the right IPS indicating that this brain area seems to be critical for automatic bottom-up magnitude processing (Cohen Kadosh et al., 2012). Study 1 of the present thesis extended this finding to the processing of relative magnitude information. In particular, to evaluate relative magnitude processing, we modulated numerical distance for symbolic and non-symbolic proportions on the neural level. In line with assumptions of the TCM, our findings suggest that relative magnitude information is processed in a notation-independent manner (Study 1). Furthermore, as an important determinant of multi-digit number magnitude, place-value integration is also associated with activation in intraparietal cortex (Wood et al., 2006). For magnitude processing of non-symbolic numerosities, Harvey, Klein, Petridou, and Dumoulin (2013) observed neural populations in the parietal cortex to be organized topographically forming numerosity maps in line with the assumptions of the TCM (but see Gebuis, Gevers, & Cohen Kadosh, 2014).

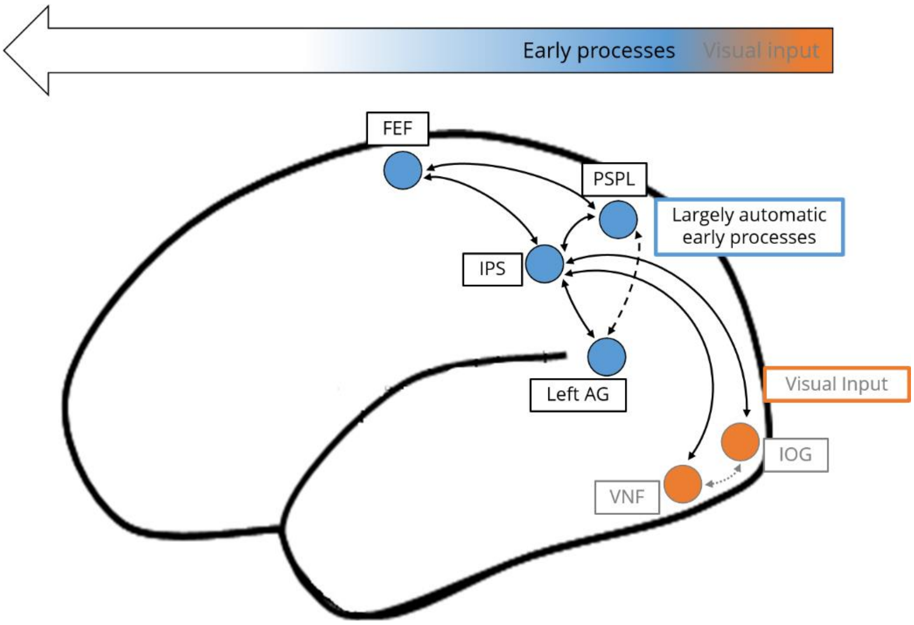

Figure 11.3: Early stimulus-driven largely automatic processes on the conceptual level of the TSA depicted in blue. They include absolute and relative magnitude processing, place-value integration and parity information in IPS, associations with space and spatial attention in PSPL and FEF, as well as retrieval of fact knowledge in left AG. These early processes in parietal regions are connected via the dorsal visual stream with initial visual input areas depicted in orange (Klein et al., 2016).

Additionally, the TCM proposes that whenever number magnitude is processed the orientation along the mental number line is reflected by activation in PSPL, a brain region typically associated with attentional navigation and spatial attention (Dehaene et al., 2003; Knops et al., 2009; see Figure 11.3). This is further substantiated by activation in frontal eye fields (FEF) during number processing reflecting (covert) shifts of attention (Simon et al., 2002; Knops et al., 2009; Corbetta et al., 1998). Thus, activation of brain areas typically involved in spatial-attentional processes reflect bottom-up automatic associations with space also on the neural level, at least in adults.

Moreover, the retrieval of fact knowledge (e.g., multiplication facts or associated labels) is also assumed to happen in a bottom-up and automatic way. The left AG was suggested to be involved in verbally mediated processes (Price, 1998, 2000). The TCM assumes that especially the retrieval of fact knowledge from long term memory is associated with activation in left AG, when arithmetic facts such as multiplication facts learned by heart are directly retrieved (Dehaene et al., 2003; Grabner et al., 2009; but see Bloechle et al., 2016; Klein, Willmes, Bieck, Bloechle, & Moeller, 2019; see Figure 11.3).

11.1.3 Neural interrelations of Stage 2

The different processes and representations associated with Stage 2 of the TSA interact with each other (as indicated by the arrows in Figure 11.3). These interrelations will be discussed in the following to evaluate the assumptions of the TSA.

The most prominent interaction is the one between numbers and space, and thus, between IPS and PSPL as already proposed in the TCM by Dehaene et al. (2003). This assumption is substantiated by the behavioral SNARC-effect which reflects that numbers are automatically associated with a specific side in space even if the processing of number magnitude is irrelevant for the task at hand (Dehaene et al., 1993; Wood et al., 2008). On the neural level, Simon et al. (2002) reported an overlap in brain activation in IPS for calculation, phoneme transcoding, and saccades which are assumed to represent (covert) shifts of attention. In line with this, Knops and colleagues (2009) showed that spatial-attentional processes are involved in mental arithmetic tasks. The authors trained a classifier to infer the direction of saccades to the left or to the right side from fMRI data. The classifier which was trained on saccades was then able to differentiate above chance level whether participants were engaged in either addition or subtraction problems based on PSPL brain activation during the calculation task: this shows that the pattern of activation during addition was similar to the pattern of activation during rightward saccades, and during subtraction similar to that of leftward saccades. The findings of Simon and colleagues (2002) and Knops and colleagues (2009) corroborate a link between numbers and space on the behavioral and neural level.

In adults who are highly experienced with different number concepts, the association of numbers and space seems to be automatic. Yet, as Study 3 of the present thesis indicated, the association between specific number concepts and space seems to develop only with increasing experience with the respective number concept. On the behavioral level, Study 3 indicated that 6th graders who just learned about multi-symbol numbers (i.e., positive and negative numbers) showed spatial associations for absolute magnitude only. In contrast to adults, they showed neither spatial associations for polarity signs (e.g., Pinhas et al., 2014), nor did they process multi-symbol numbers in a parallel componential way (Huber, Cornelsen, et al., 2014). This might result from a lack of experience with this specific numerical concept to allow for spatial associations of polarity signs and parallel processing of the components of a multi-symbol number. However, it has been shown that the level of automaticity increases with the level of numerical abilities (Cohen Kadosh et al., 2012; Girelli, Lucangeli, & Butterworth, 2000; Rubinsten, Henik, Berger, & Shahar-Shalev, 2002). Thus, with increasing experience, the association with space and the parallel processing should develop and become more pronounced resulting in an automatic association and automatic parallel processing of the components (Pinhas et al., 2014; Huber et al., 2014; Ninaus et al., 2017). On the neural level, this is further substantiated by studies of Mathieu and colleagues who found that the perception of a plus sign elicited neural activation in brain regions associated with spatial attention in adults (i.e., PSPL and FEF; Mathieu et al., 2017). However, in children comparable activation in right hippocampus – an area which is involved in spatial representations and navigation (Burgess et al., 2002; Maguire et al., 1998) – was only found in response to the plus sign by grade 7 (Mathieu et al., 2018). During development, there also seems to appear a shift from hippocampal to fronto-parietal activation in response to operation signs (Mathieu et al., 2017, 2018). These findings complement our behavioral results from Study 3 of the present thesis from a neural perspective. Furthermore, it indicates that in addition to PSPL, FEF are also involved in spatial-attentional processing.

As to my knowledge, there is no study investigating SNAs for multiplication facts on the neural level to indicate a neural interrelation between PSPL and left AG. However, behavioral data have indicated spatial associations for multiplication (Katz & Knops, 2014). The authors found an operational momentum (OM) effect for non-symbolic multiplication. The OM typically shows that participants overestimate the outcome for addition and underestimate the outcome for subtraction (e.g., McCrink, Dehaene, & Dehaene-Lambertz, 2007). Thus, they exhibit response biases in the direction of the operation. These response biases were also observed for non-symbolic multiplication and division problems: the outcomes of multiplications were over- and those of division were underestimated (Katz & Knops, 2014). The authors assumed that these biases originate from the intuition that multiplication results in larger and division in smaller outcomes. However, Shaki and Fischer (2017) found a reversed OM for symbolic multiplication and division resulting in underestimation of multiplication and overestimation of division problems. This finding might be based in an anchoring bias because the first operand in division is (on average) larger than in multiplication for identical arithmetic outcomes. Thus, the underlying mechanisms of the OM in multiplication and division might still be an open issue. In fact, multiplication fact knowledge is retrieved from long-term memory for symbolic multiplication. Thus, responses are not estimated (like in non-symbolic notations) but retrieved in symbolic notations. For this reason, the interplay between PSPL and left AG is depicted only by means of a dashed arrow (see Figure 11.3).

To evaluate the neural interrelation between IPS, in which magnitude information is processed, and left AG, in which fact knowledge is retrieved (Dehaene et al., 2003; Grabner et al., 2009), the problem size effect is considered in the following. The problem size effect describes the finding that problem difficulty increases with increasing numerical magnitude of the operands (Ashcraft & Guillaume, 2009). Thus, single-digit multiplication problems involving small numbers (e.g., 2 x 4) are responded to faster than problems involving relatively larger numbers (e.g., 8 x 9). On the one hand, this effect might originate from the fact that answers to large problems are more difficult to retrieve from long-term memory than answers to smaller problems as they are less frequently practiced and encountered (Campbell & Graham, 1985; Prado et al., 2013). On the other hand, it might also originate from differing strategy choices for solving small or large problems as large problems are less frequently solved by retrieval than small problems but rather by means of procedural strategies (LeFevre et al., 1996; Prado et al., 2013). Evidence for both explanations can be derived from temporal and spatial data on the neural level.

In an ERP study by Kiefer and Dehaene (1997), simple multiplication problems (i.e., operands ranging between 2 and 5, e.g., 2 x 4) elicited a rapidly increasing positivity over left temporo-parietal areas while this positivity rose more slowly for complex problems (i.e., operands ranging between 6 and 9, e.g., 6 x 7). With increasing processing time, both hemispheres were engaged over parietal brain regions (Kiefer & Dehaene, 1997). Furthermore, simple problems seemed to be completed after 600 msec, whereas processing time was prolonged in complex problems. In line with the TSA, the authors suggested that simple problems are rapidly retrieved in left temporo-parietal areas, while complex problems require the involvement of both hemispheres during prolonged calculation processes. Furthermore, the problem size effect was observed to activate bilateral superior temporal regions in Chinese adults who retrieved arithmetic facts from long-term memory, which correspond to the verbal code in the TCM (Prado et al., 2013; Dehaene & Cohen, 1995, 1997). In American adults, however, the problem size effect was observed in right IPS reflecting calculation procedures (Prado et al., 2013). Thus, depending on the experience with multiplication and the resulting procedure (e.g., fact retrieval vs. calculation), the neural underpinnings might differ. This, in turn, suggests that with increasing practice neural activation might shift from calculation-based IPS activation to retrieval-based temporoparietal activation. This further substantiates the link between IPS and left AG in the TSA.

11.1.4 Stage 3: Later top-down and cognitively controlled higher order processes

All processes described so far occur at the level of an individual (multi-digit or multi-symbol) number. Thus, the processed number has not yet been put into relation with other numbers so far. This happens at Stage 3 of the TSA, in which higher order processes such as working memory, cognitive control, strategy choice, planning, and goal-directed actions come into play (see green box in Figure 11.1). These executive functions play an important role in number and arithmetic processing as they are necessary to temporarily hold and manipulate relevant information in mind (Arsalidou & Taylor, 2011). At this processing stage information is retrieved, integrated, reflected, and, where necessary, manipulated and modified. This is comparable to the episodic buffer of the multi-component working memory model by Baddeley (2000) which proposed a limited-capacity temporary storage system capable of integrating information. In line with the episodic buffer, it is assumed that Stage 3 of the TSA is cognitively controlled and conscious. As such, it is controlled by the executive functions which bind necessary information for the task at hand (Baddeley, 2000).

As a first part of Stage 3, the integration (i.e., putting into relation) with previously processed numbers of the same trial or problem is assumed (see Figure 11.1). Depending on the task, digits and/or symbols within numbers as well as across numbers are encoded selectively. In eye-tracking data, this is reflected by the number of fixations within an area of interest and the location of the fixation. In fact, such selective encoding was observed in two-digit numbers (Moeller, Fischer, et al., 2009a), decimal fractions (Huber, Klein, Willmes, Nuerk, & Moeller, 2014b) as well as multi-symbol number magnitude comparisons (Huber, Cornelsen, et al., 2014). Here, specific digits and/or symbols that were decisive for the task at hand were fixated more often. Thus, top-down mediated and cognitively controlled processes guided the selective encoding of the decisive digits and/or symbols when integrating the respective number with previously processed numbers held in working memory to solve the task.

During encoding and integration of information specific procedural rules, strategies or plausibility judgments are chosen and applied. These rules require at least preliminary knowledge about the whole problem. Therefore, they are restricted to a final wrap-up stage. Thus, when the problem is complete after the integration process it will be wrapped up at this point. If not, a further processing round starts again at Stage 1, whereby the physical features of the next stimulus are extracted.

Eye-tracking data from reading research showed that measures such as total reading times and overall number of fixations provide information about late processing steps which are assumed to occur at the final wrap-up stage. This notion was substantiated by data from the number bisection task (Moeller et al., 2009b) and addition (Moeller et al., 2011b). In particular, magnitude manipulation required by bisectable triplets in the number bisection task prolonged total reading times (reflecting later top-down mediated processes), but not on gaze durations (indicating early processes; Moeller et al., 2009b) reflecting the integration of information across numbers and the verification of rules. Moreover, total reading times and refixations also increased for addition problems requiring a carry operation. Thus, these eye-tracking measures seem to reflect the wrap-up at the end of each task as the task can only be solved after all numbers of a triplet in the number bisection task are processed and after the sum of the unit digits in carry addition problems was calculated (i.e., equal to or larger than 10; for more details, see Study 4 of the present thesis). Thus, procedural rules can be applied, and plausibility checks can be made only after the whole problem is processed.

As such, at this later top-down mediated and cognitively controlled processing stage, previously processed numbers that are held in working memory are integrated, before then procedural rules and plausibility checks may be applied at a subsequent wrap-up stage. Hence, semantic number representations from Stage 2 are held in a temporary storage comparable to an episodic buffer system (Baddeley, 2000) and subsequently applied involving processes of cognitive control at Stage 3 of the TSA.

After a conclusive solution has been identified in the wrap-up stage, a response is given (see Figure 11.1). Over the course of several trials, processing and the strategies applied may be adapted. Thus, adaptation does not only occur within but also across trials (Huber, Mann, Nuerk, & Moeller, 2014; Huber, Moeller, & Nuerk, 2014; Loetscher, Bockisch, Nicholls, & Brugger, 2010). Interestingly, goal-directed adaptation of processing was also observed on the level of eye-fixation patterns. In particular, the number of fixations and total reading times increased on the decision-relevant parts of the trial, reflecting goal-directed and cognitively controlled top-down processing between trials (Huber, Mann, et al., 2014; Huber, Moeller, et al., 2014).

11.1.5 Neural instantiation of Stage 3

The TCM assumes the dorsolateral prefrontal cortex (DLPFC) to be involved in strategy choice and planning (Dehaene & Cohen, 1995, 1997). A meta-analysis by Arsalidou & Taylor (2011) provided evidence that other frontal brain regions such as inferior frontal gyrus (IFG), anterior cingulate cortex (ACC), middle frontal gyrus (MFG), and insula are also involved in numerical and arithmetic problem-solving tasks. These areas contribute to domain-general cognitive functions such as attention, cognitive control, and working memory (Arsalidou &Taylor, 2011; Fias, Menon, Szucs, 2013). This is also in line with the multi-component working memory model of Baddeley (2000) which assumes frontal brain regions to be involved in executive functions and the episodic buffer. Particularly, the IFG seems to be involved in the processing of simple numerical tasks when only a few items need to be held in working memory. When several procedural steps are required (e.g., when a carry operation is involved) or more items or stimuli have to be held in working memory, MFG seems to be involved. In more complex multi-step problems which require the application of strategies, DLPFC and superior frontal gyrus are activated (Arsalidou & Taylor, 2011). This is in line with results of Study 2 of the present thesis, in which we evaluated part-whole processing of symbolic and non-symbolic proportions. As the proportions employed (i.e., fractions, dot patterns, and pie charts) reflect bipartite part-whole relations, the structure of the respective stimuli requires that the two parts are put into relation. Thus, the clusters found for part-whole processing in Study 2 further are assumed to reflect processes of integration and setting in relation in the current model.

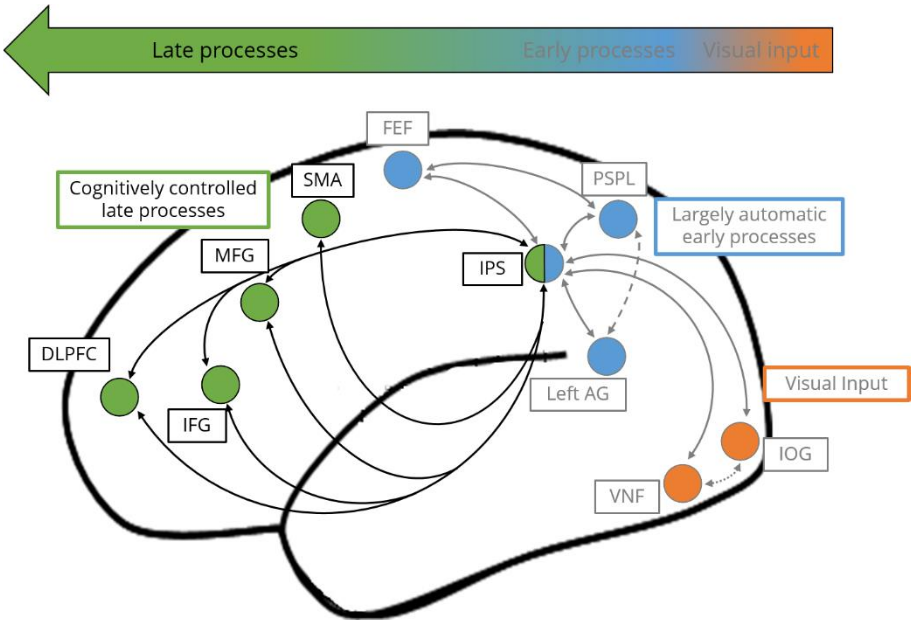

Figure 11.4: Later cognitively controlled processes of the TSA. Stage 3 of the TSA depicted in green reflects later top-down and cognitively controlled higher order processes in bilateral IPS as well as widespread frontal brain regions. They include working memory, attention, cognitive control, and goal-directed actions. These late processes in parietal and frontal regions are connected via the dorsal (arrows bent upwards) and ventral visual processing stream (arrows bent downwards) with early processes depicted in blue (Klein et al., 2016).

In line with the model proposed by Dehaene and Cohen (1997) and its later extensions by Arsalidou and Taylor (2011) and Klein et al. (2016), we found activation in bilateral middle and inferior frontal gyrus reflecting visual working memory (Song & Jiang, 2006), higher cognitive monitoring during comparing and judging (Christoff et al., 2000; Ranganath et al., 2003), procedural complexity (Delazer et al., 2003; Simon et al., 2002) and attentional processes (Ischebeck, Zamarian, Schocke, & Delazer, 2009; see Figure 11.4). Interestingly, however, we also found large clusters of activation in bilateral SMA and bilateral inferior parietal lobule (IPL) extending into bilateral occipital gyrus. Parts of activation in IPL may reflect magnitude-specific processing as shown in Study 1 of the present thesis (i.e., right IPS). However, it has been shown that the parietal cortex as part of the higher order association cortex is involved in a domain-general system of executive processes. Thus, this parietal activation might also indicate the involvement of top-down control, working memory, spatial attention, and other executive processes that go beyond pure magnitude processing but rather reflect cognitively controlled integration processes (Fias et al., 2013; Humphreys & Lambon Ralph, 2017).

This assumption was further substantiated by another analysis we conducted in Study 2, in which we found a shared neural correlate for processing symbolic and non-symbolic proportions beyond overall magnitude including dot patterns, pie charts, fractions, and decimals. Shared activation was observed in bilateral SMA and IPS, with the latter, however, being located more anterior to the magnitude-specific IPS activation found in Study 1 (Mock et al., 2019). This finding is accounted for by the split circle in IPS in Figure 11.4 indicating domain-specific automatic access of magnitude information in IPS on the one hand (Dehaene et al., 2003; Cohen Kadosh et al., 2012; Study 1) and the involvement of rather domain-general higher order processes in more anterior IPS regions on the other hand (Study 2).

Importantly, it has been shown that specific neurons in the IPS are tuned to specific numerosities (Nieder, 2006; Roitman et al., 2007). Thus, specific substructures of the intraparietal cortex seem to be involved in domain-specific magnitude processing. Furthermore, a recent study by Castaldi and colleagues (2019) found that the IPS showed subregional specialization for number perception and numerical operations, respectively. Interestingly, this is also reflected by the results of the RSA in Study 2, which indicated similarities in the activation patterns of a specific brain region (Kriegeskorte et al., 2008). We found that the neural patterns in bilateral IPL were very similar for proportions with part-whole relations (i.e., fractions, dot patterns, and pie charts), but not for decimals. In line with DeWolf and colleagues (2016), we concluded that the underlying neural processes reflect the bipartite structure of those part-whole relations. Thus, the integration and putting into relation of the bipartite proportions was reflected even in the activation pattern within bilateral IPL. This corroborates the finding that intraparietal regions are involved in both domain-specific and domain-general processes: Decimals simply and directly reflect their number magnitude in a base-10 notation and do not require additional processing of proportional aspects.

Bipartite part-whole structures as fractions, dot patterns, and pie charts, however, require the relating of their two parts. This, in fact, is reflected in the activation pattern as revealed by the RSA. Thus, in combination with the results of Study 1 of the present thesis and recent literature on domain-specific magnitude processing, these results indicate that intraparietal regions are involved in both domain-specific magnitude as well as domain-general processing beyond magnitude as reflected in Figure 11.4.

11.1.6 The resulting model extension

The aim of the extension was to integrate aspects of temporal dynamics with neural correlates of domain-general and domain-specific numerical processes to better understand the underlying processes involved in visual number processing – combining evidence with good spatial resolution as provided by functional imaging methods (principally independent from temporal aspects and time-critical methods) with evidence with good temporal resolution as provided by eye-tracking methods (based on findings of time-critical methods). Figure 11.5 depicts the full resulting model extension.

The successively added cortex areas in the TSA result in a large network which is involved in number processing. In particular, visual number processing starts with the extraction of physical features in occipitotemporal brain regions (depicted in orange as Stage 1), followed by a largely automatic early stimulus-driven processing stage at the conceptual level in parietal regions (depicted in blue as Stage 2) and complemented by later higher order top-down and cognitively controlled processes in fronto-parietal areas (depicted in green as Stage 3) connected via dorsal and ventral processing streams (Klein et al., 2016; Klein, Moeller, Glauche, Weiller, & Willmes, 2013). These processing steps finally result in three stages describing aspects of the temporal dynamics and neural processes involved in numerical cognition in an extended version of the TCM (see Figure 11.5).

Interestingly, this network corresponds quite closely to the neural network proposed for the multiple demand system (MD; Duncan, 2010; Fedorenko et al., 2013) and the extrinsic mode network (EMN; Hugdahl et al., 2015), which assume the involvement of diverse domain-general areas and processes in interaction with smaller domain-specific subregions for complex cognitive processes. These networks include joint activation of DLPFC including inferior and middle frontal gyrus, insula, precentral gyrus, SMA, and areas in and around the IPS (Duncan, 2010; Fedorenko et al., 2013).

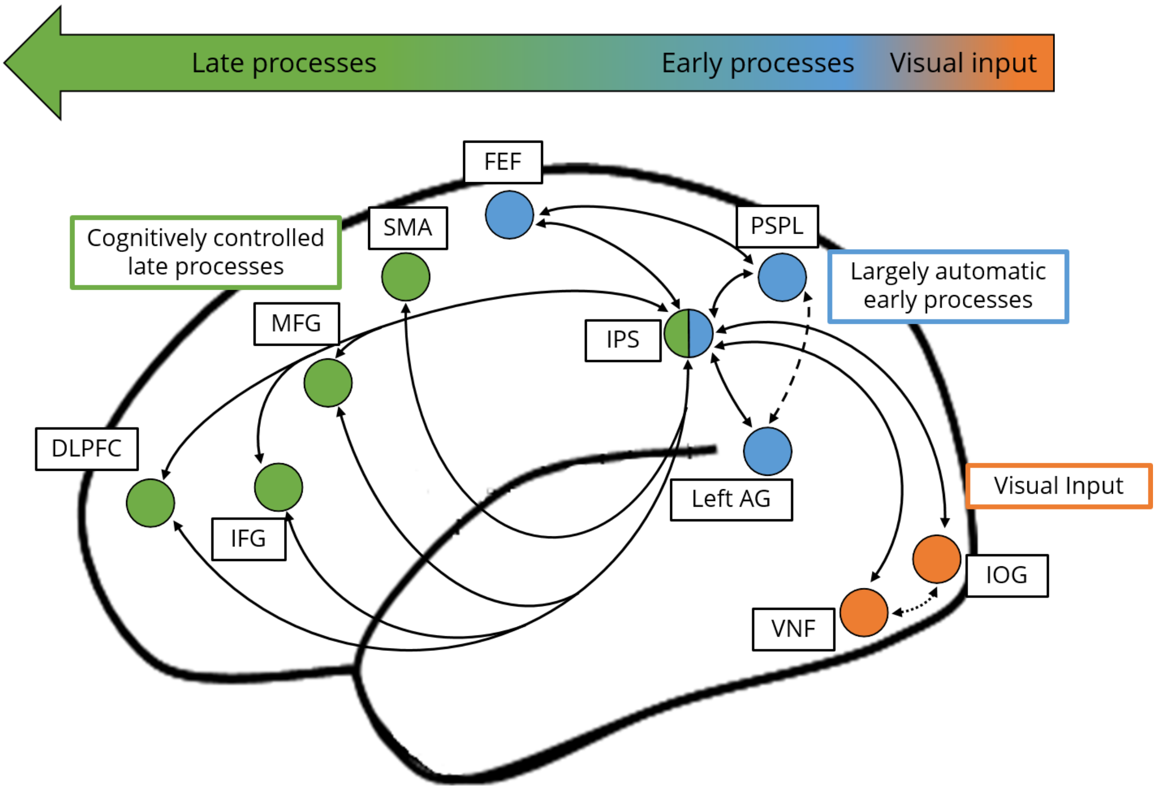

Figure 11.5: Extension of the TCM by the Three Stages Account (TSA). In orange, initial visual input processes are involved in the extraction of physical features in Stage 1. In Stage 2, early stimulus-driven and largely automatic processes on the conceptual level take place in parietal brain regions depicted in blue. In Stage 3, higher order top-down and cognitively controlled processes complement number processing in fronto-parietal areas depicted in green. The different brain areas are connected via dorsal (arrows bent upwards) and ventral visual stream (arrows bent downwards; Klein et al., 2016).

The MD is associated with various cognitive and executive control demands including perception, memory processes, language, problem solving, task novelty, and response selection independent of the respective task (Duncan, 2010, 2013; Fedorenko et al., 2013). The EMN extends these functions by including focused attention, goal maintenance, strategy selection, working memory, and performance monitoring (Hugdahl et al., 2015). Thus, MD and EMN describe broad functional generality on the neural level. Importantly, these areas and functions are quite similar to the ones proposed in the TSA (see Figure 11.5). However, it is important to note here that it is not assumed that complex cognitive tasks such as number processing or mental arithmetic are associated with domain-general functions only, which support a variety of cognitive functions independent of the actual task at hand. Rather, the widespread neural network of domain-general functions is complemented by highly specialized domain-specific cognitive and neural mechanisms (Fedorenko et al., 2013).

This is substantiated by our findings of Study 1 and 2. While Study 1 revealed domain-specific magnitude processing of proportions in a small cluster in right IPS (Mock et al., 2018), complementary data of Study 2 provided a widespread neural network including frontal, parietal and occipital brain regions involved in processing of part-whole relations and a larger shared intraparietal cluster for proportion processing beyond overall magnitude (Mock et al., 2019). Thus, our findings are in line with recent research on neurocognitive mechanisms in complex cognitive tasks.

Furthermore, the TSA enriches previous literature by combining the neural underpinnings and aspects of temporal dynamics of numerical cognition. A recent study by Daitch and colleagues (2016) further substantiated several assumptions for Stage 1 and Stage 2 of the TSA by means of ECoG recordings. First, the authors showed that populations of neurons in the VNF area responded selectively to the visual presentation of individual numbers. Second, they found that a subregion of the IPS was selectively activated when subjects actively manipulated number magnitude. This subregion was anatomically similar to parietal areas involved in numerosity tuning (Harvey et al., 2013; Piazza et al., 2004). In contrast, a more posterior site in IPS was associated with rather domain-general and less-selective responses supporting the assumptions of TSA for both domain-specific and domain-general processes in parietal areas (Daitch et al., 2016; Study 2). Third, and most importantly, Daitch and colleagues (2016) were able to distinguish between early visual processing in the VNF area and later magnitude related processes in a subregion of the IPS. Furthermore, a recent MEG study supports the notion of the TSA that visual number processing evolves across time from posterior to anterior brain regions (Pinheiro-Chagas et al., 2018; see also Dehaene, 1996). Thus, in line with recent literature, the TSA offers a first step towards a better understanding of the ongoing spatiotemporal processes and mechanisms involved in visual number processing.

11.2 Evaluating TSA by means of neuropsychological data

In the following, the assumptions of the TSA will be briefly evaluated by means of neuropsychological data for each proposed stage as this model extension should be able to explain not only typical numerical performance, but also impaired performance of patients with specific brain lesions.

The advantage of functional imaging is that it is a non-invasive method to observe the involvement and interrelation of distinct brain areas in different cognitive tasks. Its good spatial resolution allows for conclusions about small subregions as well as larger networks involved in cognitive processes. However, functional imaging only reveals correlations of specific tasks and specific brain activations. Yet, it does not allow for causal inferences. In contrast, lesion studies address associations of damaged brain regions with deficits to indicate which structures are essentially required for which cognitive processes, and thus, allow for causal association between brain and behavior (Müller & Knight, 2006). Unfortunately, to my knowledge there is no data on temporal aspects of impaired number processing. For this reason, this section focuses on the spatial structure-function-relationships proposed by the TCM and the TSA.

11.2.1 Evaluating deficits in visual input processing at Stage 1

At the initial visual input stage of the TSA, physical features of symbolic stimuli are extracted in the visual number form area in occipital brain regions in line with the TCM. In this brain region, visual properties (e.g., shape) and spatial relationships (e.g., relative positions) of numbers are extracted and processed (Cohen & Dehaene, 1991). Thus, the TCM and the TSA predict that lesions in the visual number form area should result in deficits in the recognition of visually presented numbers or visual features of the numbers. This is in line with data from a patient who suffered from visual agnosia showing impaired recognition of visual numbers in the absence of visual-sensory deficits or other cognitive impairments (Pesenti et al., 2000). Pesenti and colleagues observed an impairment of visual processes as physical judgments of numbers were impaired while numerical processes (e.g., comparison, parity judgments) were preserved. The patient had severe problems dealing with the visual shape of digits when generating Arabic numbers from memory. Hence, he showed a clear dissociation: while semantic numerical processing and calculation were preserved, visual Arabic representations were impaired due to his visual agnosia. Furthermore, physical features of digits are often not extracted appropriately in patients with lesions in left occipito-temporal regions as digits are misidentified or read wrongly (Dehaene & Cohen, 1995).

11.2.2 Evaluating deficits in conceptual functions at Stage 2

The second processing stage of the TSA involves three parietal areas as proposed by the TCM (Dehaene et al., 2003). At this stage, specific semantic aspects are assigned to the visual stimuli at the conceptual level: Magnitude (Dehaene & Cohen, 1995, 1997; Dehaene et al., 2003; Mock et al., 2018; Piazza et al., 2007), place-value (Guilherme Wood, Nuerk, & Willmes, 2006), and parity information (Klein et al., 2010) are supposed to be represented in intraparietal areas, an association between numbers and space to be built in PSPL (Dehaene et al., 2003), and fact knowledge to be stored in left AG (Dehaene et al., 2003; Grabner et al., 2009; but see Bloechle et al., 2016; Klein et al., 2019). Thus, lesions in these different parietal areas should lead to impairments of different functions.

For instance, the TCM and the TSA propose that the association of numbers and space goes hand in hand with activation in PSPL, a brain region typically associated with attentional navigation and spatial attention (Dehaene et al., 2003; Knops et al., 2009). This is in line with data from patients suffering from spatial neglect. Patients with unilateral neglect resulting from a (right) parietal lesion show a spatial deficit when stating the midpoint of two numbers without calculating (e.g., midpoint between 11 and 19; Zorzi et al., 2002). Their suggested midpoint was significantly shifted to the right on the mental number line supporting the idea of a strong relationship between numbers and visuo-spatial representations and attention (Zorzi et al., 2002; Zorzi et al., 2012; for a review, see Umiltà et al., 2009). Furthermore, damage in posterior parietal cortex can also result in deficits in spatial working memory (Pisella, Berberovic, & Mattingley, 2004). In line with this, it was also shown that brain lesions in this area are commonly associated with deficits in ordering and rearranging information held in working memory (Koenigs, Barbey, Postle, & Grafman, 2009; Wager & Smith, 2003). This impairment might reflect deficits in the monitoring and manipulation of objects in visual space (Koenigs et al., 2009; Pisella et al., 2004). In fact, this further substantiates the assumptions of the TCM and its extension of the TSA for the PSPL reflecting attentional navigation.

For the retrieval of fact knowledge (e.g., multiplication facts) it was shown that language-based representations are required because multiplication tables are typically learned by verbal rote memorization. In fact, patients with impaired multiplication fact knowledge typically also show an associated aphasia (Dehaene & Cohen, 1997; for more detail, see Dehaene et al., 2003). Thus, arithmetic fact knowledge such as overlearned multiplication facts seem to be subserved by a verbal circuit in contrast to arithmetic operations which require quantity manipulations (e.g., subtraction) in a quantity circuit (Dehaene et al., 2003).

This latter quantity circuit involves intraparietal brain regions as proposed by the TCM and the TSA. Thus, the model predicts that lesions in intraparietal brain regions should result in deficits in magnitude processing. Supporting this notion, it has been shown that number processing can be severely impaired following lesions or degenerative diseases in intraparietal areas, while language and semantics of words can be preserved reflecting a separate semantic representation for number magnitude (Cipolotti, Butterworth, & Denes, 1991; Dehaene & Cohen, 1997; Dehaene et al., 2003; Delazer, Karner, Zamarian, Donnemiller, & Benke, 2006).

11.2.3 Evaluating deficits in top-down and cognitively controlled processes at Stage 3

At Stage 3 of the TSA, cognitively controlled integration processes are assumed reflecting domain-general processes like top-down control, working memory, spatial attention, and other executive processes that go beyond magnitude processing (Fias et al., 2013; Humphreys & Lambon Ralph, 2017). Besides frontal brain regions like PFC, IFG, MFG, and SMA, the TSA assumes these processes to be subserved also by intraparietal areas (in contrast to the TCM) reflecting a widespread fronto-parietal network. Thus, the TSA predicts that lesions in these brain areas should result in deficits in the associated top-down mediated processes and executive functions. In fact, lesions in the posterior part of the IPS can cause spatial-attentional deficits (Gillebert et al., 2011). Furthermore, lesions in inferior parietal areas often lead to impairments of verbal information held in working memory (Baldo & Dronkers, 2006). This, in turn, supports the notion of the IPS being involved in domain-general top-down processes such as working memory from a neuropsychological perspective. Additionally, Baldo and Dronkers (2006) showed that patients with inferior frontal lesions were impaired in the maintenance and rehearsal of information held in working memory. Executive functions are disrupted by lesions in prefrontal areas (Baldo & Dronkers, 2006; Baldo & Shimamura, 2000). The TCM proposes that prefrontal areas are involved in planning and strategy choice necessary for numerical cognition (Dehaene & Cohen, 1995, 1997). Owen and colleagues (1990) substantiated this assumption showing that patients with lesions in prefrontal areas exhibit deficits in higher level planning abilities and the use of strategies. Furthermore, it has been shown that PFC is also critically involved in monitoring and manipulating information held in working memory. Patients with lesions in this brain region often have difficulties to perform self-ordered working memory tasks in which they were asked to choose a different stimulus of an arrangement of stimuli in every trial until all stimuli have been chosen (Petrides, 1995; Petrides & Milner, 1982; see Szczepanski & Knight, 2014 for a review). Thus, PFC seems to be involved in the rearrangement, transformation, and manipulation of information held in working memory. This is in line with assumptions of the TSA proposing the integration and putting into relation of information at a later top-down mediated processing stage.

This later processing stage also involves cognitive control to perform goal-directed actions. In patients with lesions in SMA, cognitive control as well as task and rule switching abilities were observed to be impaired (Nachev, Kennard, & Husain, 2008). This supports the notion of TSA that SMA is also involved in later top-down mediated and cognitively controlled processes.

In sum, neuropsychological data providing support for causal structure-function relationships substantiate the assumptions of the TSA as a possible extension of the TCM, at least for spatial structure-function-relationships. However, it needs to be mentioned that deficits or impairments in cognitive functions might not only be due to lesions in specific brain areas, but also because several areas are disconnected, affecting a larger network (Müller & Knight, 2006).

11.3 Developmental aspects of TSA

In the following, developmental aspects of TSA will be discussed briefly. However, the following elaborations on potential developmental aspects need to be considered with caution as the TSA is mainly based on data from adults.

With regards to the three processing steps, I assume that processes at each stage need to develop over time. Starting with the initial visual input stage, a distinction between non-symbolic and symbolic quantities needs to be made: whereas infants already perceive and process non-symbolic numerosities (Izard, Sann, Spelke, & Streri, 2009; Lipton & Spelke, 2003, 2004; Xu & Arriaga, 2007; Xu, Spelke, & Goddard, 2005), children learn about symbolic numbers not until kindergarten or preschool. Importantly, on the neural level, 4-year-old children processed non-symbolic numerosities similar to adults (Cantlon, Brannon, Carter, & Pelphrey, 2006). However, for symbolic numbers, it was only possible for children to assign symbols their specific numerical meaning after they were introduced to this concept (Li et al., 2018).

Comparable to early word learning, the acquisition of number semantics might be driven by external characteristics of numbers such as their frequency (Saffran, Aslin, & Newport, 1996). Accordingly, effects related to number-specific characteristics at the second processing stage of early stimulus-driven processes (e.g., frequency effects, Brysbaert, 1995; association with space, Study 3) should only occur after children master the assignment of the respective semantic attributes to single- and multi-digit as well as multi-symbol numbers. With increasing experience, symbols and their corresponding numerical characteristics should be stored in long-term memory. From then on, these characteristics can be accessed and assigned to the perceived symbols more and more automatically whenever a number is encountered (Henik & Tzelgov, 1982). In children with developmental dyscalculia, this early stimulus-driven processing stage might lack automation (Moeller, Neuburger, Kaufmann, Landerl, & Nuerk, 2009). On the neural level, symbolic number processing is associated with activation in parietal brain areas in adults (see above). Children, however, rather engaged frontal regions indicating a shift from strong involvement of frontal areas associated with domain-general processes to increased automation of symbolic number processing in intraparietal and posterior parietal regions (Ansari, Garcia, Lucas, Hamon, & Dhital, 2005; Rivera, Reiss, Eckert, & Menon, 2005; see Kaufmann, Wood, Rubinsten, & Henik, 2011 for a meta-analysis). This development reflects the maturation and specification of neural networks for symbolic number processing in children's brains leading to the neural basis for largely automatic number processing, as indicated by the second stage of the TSA. Thus, with increasing age there is a shift of activation from frontal domain-general number-unspecific brain areas to number-related (intra)parietal regions. This further indicates that children rely on parietal regions only with increasing age and experience. Thus, after visual input processing of Stage 1 children might skip the proposed Stage 2 of the TSA (as it might not be available yet) and process numbers in a cognitively controlled top-down manner, until they are experienced enough with numbers and their semantics. Only then processing might be automatic and activation shifts from frontal to parietal areas. Afterwards, frontal areas might be recruited for working memory and the application of rules, for instance, during mental arithmetic as proposed for Stage 3 of the TSA. Yet, experience with the manipulation of numbers is needed (Moeller, Klein, & Nuerk, 2011a). Thus, on both the behavioral and the neural level, processes are assumed to become more specific with increasing experience (Kaufmann et al., 2011; Rivera et al., 2005 Moeller et al., 2011b). During arithmetic calculation tasks, children recruited similar neural networks including frontal and parietal brain regions as compared to adults (Davis et al., 2009). Thus, the respective neural networks might already be in place in children, however, the patterns of activation in the parietal cortex differed significantly as a function of age (Davis et al., 2009). Thus, with increasing age and experience the parietal cortex becomes more specialized and frontal brain regions might rather serve as supportive areas being involved in working memory, planning, and strategy choice (Kucian, Von Aster, Loenneker, Dietrich, & Martin, 2008).

12 Future directions

Extending the TCM by the TSA only provides a first step towards describing the complex processes involved in numerical cognition more comprehensively by integrating both aspects of temporal dynamics and corresponding neural correlates of the processes involved. Nevertheless, the TSA remains a tentative account based on the synthesis of the present findings and the existing literature. For this reason, future research is needed to further evaluate the validity of the present account. To pursue this endeavor, I will provide some research ideas for future studies in the following that might help to evaluate and test the TSA in the following.

a) The most obvious question concerns the spatio-temporal processing of numbers. So far, non-invasive neuro-cognitive research on numerical cognition was conducted either with good spatial resolution by means of fMRI or with good temporal resolution by means of EEG, ERPs, MEG, or eye-tracking. Yet, combined considerations of spatio-temporal number processing are scarce. Research on numerical cognition would, however, benefit from such combined measures to better understand the underlying processes. To evaluate the assumptions of the TSA and further gain insights into spatiotemporal number processing, the verification version of the number bisection task (NBT) might be used employing fMRI- and EEG-measures simultaneously. In this task, participants are asked to indicate whether the second number of a triplet corresponds to the arithmetic integer mean of the interval defined by the two outer numbers (e.g., 3_5_7) or not (e.g., 3_6_7). Several number representations and the application of those representations are involved in the NBT: magnitude processing, processing of fact knowledge in multiplicative triplets, and the application of procedural rules (Moeller, Fischer, et al., 2009b; Nuerk et al., 2002; Guilherme Wood, Nuerk, et al., 2008). Importantly, these different representations and their application reflect different processing stages according to the TSA. While magnitude and fact knowledge are assumed to be processed at an early stimulus-driven and largely automatic processing stage, procedural rules might rather be applied at a later top-down and cognitively controlled processing stage. Thus, this task seems well suited to evaluate and test the assumptions of the TSA. For this reason, three different stimulus types should be used: first, multiplicative triplets (e.g., 21_24_27) to evaluate the processes involved in magnitude and fact processing, second, bisectable, but non-multiplicative triplets (e.g., 21_25_29) to enforce magnitude manipulations and computations, and third, non-bisectable triplets (e.g., 23_25_28, the correct mean would be 25.5) to violate the rule. According to the TSA, multiplicative triplets should activate IPS and left AG, reflecting the retrieval of magnitude information and fact knowledge (Wood et al., 2008; Dehaene et al., 2003). Furthermore, these processes should occur early. In line with this, automatic magnitude processing was shown to occur at about 170 to 200 ms after stimulus onset in EEG measures (Dehaene, 1996; Hsu & Szűcs, 2012). Additionally, bisectable but not multiplicative triplets should more strongly engage intraparietal and frontal regions requiring magnitude manipulations. Here, however, early and later processing steps should be reflected in the EEG-signal indicating early automatic magnitude processing at about 170 to 200 ms and later higher order processing at about 400 ms (Hsu & Szűcs, 2012). In contrast, non-bisectable triplets should rather activate frontal brain areas reflecting higher cognitive monitoring and cognitive set changes because of rule violation. However, the rule violation might be already detectable early because the parity of the two outer numbers is not the same. Nevertheless, later plausibility judgments might occur and reflect top-down mediated processes according to the TSA (Christoff et al., 2000; Guilherme Wood, Nuerk, et al., 2008). In the EEG-signal, a later component at about 600 ms might indicate rule violations comparable to syntactic violations in language processing (P600; Gouvea, Phillips, Kazanina, & Poeppel, 2010; Kaan & Swaab, 2003), reflecting the application of rules and plausibility judgments at the wrap-up stage of the TSA.

Importantly, a multimodal data fusion approach (Huster, Debener, Eichele, & Herrmann, 2012) may be applied to benefit from both fMRI and EEG measurements as well as to integrate and combine the insights gained. This method uses information of both modalities to explore the full spectrum of available information. To pursue this, the two signals are first processed separately (reducing the need of simultaneous acquisition of both methods; Huster et al., 2012). Afterwards fMRI statistical maps and ERPs of all subjects are merged and analyzed jointly. This approach provides “a joint spatiotemporal decomposition with joint independent components corresponding to electrophysiologically measured responses (indicating the timing of signal changes) alongside associated clusters of active regions (indicating spatial origins of signal changes)" instead of having either temporal or spatial data (Huster et al., 2012, p. 6057). This results in the mapping of time courses reflected by ERPs alongside their associated spatial correlates and vice versa allowing for a more comprehensive view on the processes involved in the NBT. Importantly, in this way the assumptions of the TSA can be validated by combining spatial (fMRI) and temporal (ERPs) data within one single task.

b) As part of the higher order association cortex, the IPS was shown to be involved in a variety of domain-general tasks (Critchley, 1953; Culham & Kanwisher, 2001; Humphreys & Lambon Ralph, 2015, 2017; Simon et al., 2002). However, it is also assumed that at least a subregion of IPS is involved in domain-specific numerical tasks (Nieder et al., 2006; Mock et al., 2018). Yet, in more complex numerical tasks such as proportion processing both domain-general and domain-specific processes are required to solve the task at hand. In Study 2 of this thesis, we found processes involved in proportion processing related to, but beyond overall magnitude processing, associated with parietal activation. However, with the design of Study 2, it was not possible to disentangle the domain-general parietal processes involved in proportion processing. Based on the existing literature, we assumed visuospatial attention, numerical computations and calculations, working memory, and eye-movements to be involved (Humphreys & Lambon Ralph, 2015, 2017; Simon et al., 2002; Mock et al., 2019). However, to disentangle actually involved processes, I outline two research ideas in the following.

First, following the idea of Simon and colleagues (2002), different tasks can be employed covering a range of cognitive functions in fMRI: eye movement, visual attention, and subtraction tasks, respectively, used in Simon et al. (2002), a size congruity task to account for automatic magnitude processing (Cohen Kadosh et al., 2012; Kaufmann et al., 2005), and a matching-to-sample task to examine working memory (Müller & Knight, 2006; Paule et al., 1998). Activations found for these tasks may then be compared to the activations found for proportion processing related to, but beyond overall magnitude processing of Study 2. In doing so, it should be possible to investigate the neural overlap of the respective process with proportion processing in bilateral IPL, the region identified in Study 2, by means of a conjunction analysis. Based on this, additional multivariate analyses (e.g., multivariate pattern analysis for common features or RSA to differentiate between processes) would provide insights into the complex interrelation between proportion processing and the respective cognitive function (e.g., visual attention, automatic magnitude processing, calculation, working memory, or eye movements) in parietal brain regions.

Second, another possibility would be to apply transcranial magnetic stimulation (TMS) to bilateral IPL and to ask participants to solve the above-mentioned tasks. When activation in bilateral IPL found for proportion processing related to, but beyond magnitude processing reflects the involvement of other cognitive functions as assumed in Study 2, participants might be specifically impaired in the respective task, because the underlying cognitive function should be inhibited by TMS.

13 Conclusion

The extension of the Triple Code Model (TCM) by the Three Stages Account (TSA) as put forward in the present thesis provides a first attempt to complement neurofunctional correlates of domain-specific numerical and domain-general processes with aspects of temporal dynamics of number processing.

The TCM is the most influential model to describe processes involved in numerical cognition by assigning structure-function-relationships on the neural level. Yet, as a structural model, its focus was less on domain-general processes or temporal aspects of number processing involved. To pursue this issue, the present thesis aimed at specifying the assumptions the TCM makes about domain-specific numerical and domain-general parietal processes involved in visual number processing (principally independent from temporal aspects and time-critical methods) and extending the scope of the TCM by enriching the model with early bottom-up and later top-down mediated processing stages (based on findings from time-critical methods). In doing so, it was possible to derive three subsequent processing stages: an initial visual input stage in occipital brain areas, in which physical features of the stimuli are extracted, an early largely automatic stimulus-driven processing stage associated with parietal regions, in which conceptual and semantic information is assigned to the stimuli, and a later top-down and cognitively controlled processing stage attributed to fronto-parietal areas, in which stimuli are put into relation and procedural rules are applied. The current model extension of the TSA reflects a large network of domain-general processes in occipital, parietal and frontal brain areas supporting and complementing highly specialized domain-specific subregions involved in numerical cognition.

Nevertheless, the TSA remains a first tentative account based on the synthesis of the present findings and the existing literature. Future research is needed to further evaluate the validity of the present account. Nevertheless, the TSA represents a first approach to a better understanding of the processes involved in numerical cognition as it is the first account to combine both the neuro-functional correlates *as well as* aspects of their temporal dynamics. Future modifications and extensions of the TCM should therefore not only consider domain-specific and domain-general processes involved in numerical cognition, but also integrate spatial and temporal aspects to allow for a better understanding of the complex processes and their interrelations in the human brain.

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Erklärung

Hiermit erkläre ich, dass ich die vorliegende Arbeit selbstständig und ohne Benutzung anderer als der angegebenen Hilfsmittel angefertigt habe. Alle Stellen, die wörtlich oder sinngemäß aus veröffentlichten oder nicht veröffentlichten Schriften entnommen wurden, sind als solche kenntlich gemacht. Die Arbeit ist in gleicher oder ähnlicher Form oder auszugsweise in einer anderen Prüfung noch nicht vorgelegt worden; auch wurde mit dieser Arbeit oder einer anderen Dissertation noch kein Promotionsversuch unternommen.

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Tübingen, den 27. Juni 2019