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Abstract

A basic capacity for tracking and mentally representing the exact numerosity of up to four concurrently perceived objects, as well as the capacity to approximately estimate differences in numerical magnitude, appears to constitute an evolutionarily predisposed “number sense” in humans and non-human animals. Due to its nonsymbolic nature, the number sense allows us to determine that two marbles are less numerous than four marbles (●● versus ●●●●), without the use of language and explicit counting. Influential theoretical frameworks in the field of numerical cognition argue that these basic, *core-cognitive* capacities provide a foundation for the uniquely human development of symbol-based number processing abilities. Such abilities include communicating quantitative information in speech (e.g., “look at the *two birds* over there!”) and writing (e.g., a price tag indicating that a shirt costs “\$20”), as well as applied uses of number in fields such as mathematics (e.g., “ $1 + 1 = 2$ ”). The evolutionarily inherited number sense has been argued to give symbolic numbers their meaning and representational content (i.e., semantics), by virtue of associating a number of perceived objects (e.g., ●●) to their corresponding symbolic referent (e.g., “two” and “2”).

Alternative proposals suggest that symbolic number processing abilities develop independently of basic nonsymbolic number processing abilities. Instead, attributing meaning to a number may depend on learning the order of the numerical count-list (i.e., “1, 2, 3, 4, ...”) and realizing that a given number (e.g., 5) is “one more” than its preceding neighbor. Determining which of these proposals most adequately correspond to the brain’s acquisition and representation of numerical information may provide important insights for the development of educational mathematics curricula, as well as for interventions designed to support a basic level of numeracy across the lifespan. To this end, the current thesis investigated the neurocognitive foundations of basic number processing abilities in typically developing children and adults. Three overarching research

questions provided a common basis for the studies: how does the brain process different numerical representations? Is this processing dependent on shared neurocognitive mechanisms? What are the effects of biological and cognitive maturation on numerical processing abilities?

Four neuroimaging studies provide neural biomarkers for the successful acquisition and deployment of numerical cognition, acting as a baseline for future research. Together, Papers I–IV indicate that: symbolic numbers increasingly acquire semantic reference in relation to other symbols over developmental time; nonsymbolic numerical magnitude may be manipulated asemantically through basic visuospatial processing; neurocognitive mechanisms for numerical magnitude processing begin reaching adult-level maturity around 11 years of age; numerical ordering and magnitude discrimination abilities are supported by independent neurocognitive mechanisms but jointly depend on visuospatial working memory; and that neurocognitive maturation effects govern the development of executive functions and lexico-semantic abilities for symbolic number processing, important for arithmetic abilities. These results provide the basis for outlining a tentative, *P versus A-conscious Number processing* (PAN) model with testable predictions for future research, supporting the view of independent symbolic and nonsymbolic numbers.

Keywords: Numerical cognition, fMRI, triple code model, cardinality, ordinality, functional connectivity, development.

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Abbreviations

ACC	Anterior cingulate cortex
AG	Angular gyrus
AI/AIns	Anterior insula
ANS	Approximate number system
BOLD	Blood-Oxygen-Level Dependent
CPM	Connectome-based Predictive Modeling
DAN/VAN	Dorsal/ventral attention network
DLPFC	Dorsolateral prefrontal cortex
fMRI	Functional Magnetic Resonance Imaging
fcMRI	Functional Connectivity Magnetic Resonance Imaging
IFG	Inferior frontal gyrus
IPS	Intraparietal sulcus
MCC	Middle cingulate cortex
MFG	Middle frontal gyrus
MNI	Montreal Neurological Institute (brain atlas)
MNL	Mental number line
MTG	Middle temporal gyrus
OTS	Object-tracking system
PAN	P versus A-conscious Number processing model
pMFC	Posterior-medial frontal cortex
RBC	Region of Interest-Based Connectivity
ROI	Region of Interest
SFG	Superior frontal gyrus
SMA	Supplementary motor area
SMG	Supramarginal gyrus
STG	Superior temporal gyrus
TCM	Triple Code Model (of numerical cognition)
vm-/vIPFC	Ventromedial/ventrolateral prefrontal cortex

List of papers

The following papers, hereafter referenced by their Roman numeral, comprise the foundation of this thesis.

- I. Skagenholt, M., Träff, U., Västfjäll, D., & Skagerlund, K. (2018). Examining the Triple Code Model in numerical cognition: An fMRI study. *PLOS ONE*, 13(6), eo199247. Published under CC-BY license.
- II. Skagenholt, M., Skagerlund, K., & Träff, U. (2021). Neurodevelopmental differences in child and adult number processing: An fMRI-based validation of the triple code model. *Developmental Cognitive Neuroscience*, 48, 100933. Published under CC-BY license.
- III. Skagenholt, M., Skagerlund, K., & Träff, U. (2021). Neurodevelopmental differences in task-evoked number network connectivity: Comparing symbolic and nonsymbolic number discrimination in children and adults. *Under review*.
- IV. Skagenholt, M., Skagerlund, K., Träff, U. (2021). Connectome-Based Predictive Modeling Indicates Dissociable Neurocognitive Mechanisms for Numerical Order and Magnitude Processing in Children. *Manuscript*.

Contents

ABSTRACT I

ACKNOWLEDGEMENTS III

ABBREVIATIONS..... V

LIST OF PAPERS VI

1. INTRODUCTION 9

1.1. THE NUMBER SENSE AND NONSYMBOLIC NUMBER 11

1.1.1. *The object tracking system* 12

1.1.2. *The approximate number system* 13

1.1.3. *Connecting the dots: the MNL, ANS, and IPS* 14

1.2. THE SYMBOLIC REFERENCE GAP AND SYMBOLIC NUMBER 16

1.2.1. *OTS bootstrapping* 18

1.2.2. *ANS bootstrapping*..... 18

1.2.3. *Mixed evidence for ANS bootstrapping*20

1.3. COGNITIVE DOMAIN-SPECIFICITY AND DOMAIN-GENERALITY..... 21

1.3.1. *The overlapping nature of magnitude processing*23

1.3.2. *Executive functions influence number processing*.....25

1.3.3. *Separable systems of number processing?*26

1.4. THE TRIPLE CODE MODEL..... 27

1.4.1. *The primacy of analog magnitude*28

1.4.2. *Symbolic number and semantic reference*.....29

1.5. NUMERICAL MAGNITUDE AND NUMERICAL ORDER 31

1.5.1. *The case for separate cardinal and ordinal systems* 31

1.5.2. *Implications for numerical cognition*32

2. AIMS34

2.1. PAPER I 34

2.2. PAPER II 35

2.3. PAPER III..... 36

2.4. PAPER IV 36

3. METHODS..... 38

3.1. PARTICIPANTS38

3.1.1. <i>Ethical considerations</i>	39
3.2. FMRI	40
3.3. EXPERIMENTAL DESIGN AND STIMULI	41
3.3.1. <i>Behavioral study design</i>	41
3.3.2. <i>Neuroimaging study design</i>	42
4. SUMMARY OF PAPERS	46
4.1. PAPER I	46
4.1.1. <i>Background and aims</i>	46
4.1.2. <i>Methods</i>	48
4.1.3. <i>Results and Discussion</i>	50
4.2. PAPER II	52
4.2.1. <i>Background and aims</i>	52
4.2.2. <i>Methods</i>	55
4.2.3. <i>Results and Discussion</i>	56
4.3. PAPER III	60
4.3.1. <i>Background and aims</i>	60
4.3.2. <i>Methods</i>	62
4.3.3. <i>Results and Discussion</i>	63
4.4. PAPER IV	65
4.4.1. <i>Background and aims</i>	65
4.4.2. <i>Methods</i>	68
4.4.3. <i>Results and Discussion</i>	70
5. GENERAL DISCUSSION	75
5.1. MAIN FINDINGS	76
5.1.1. <i>What is the role of the intraparietal sulcus?</i>	77
5.1.2. <i>Towards a reinterpretation of the IPS for number</i>	79
5.1.3. <i>IPS responds to numerosity in the absence of tasks</i>	80
5.1.4. <i>Numerical cognition and executive functions</i>	82
5.2. P VERSUS A-CONSCIOUS NUMBER PROCESSING MODEL	84
5.2.1. <i>Future research on the PAN model</i>	91
5.3. LIMITATIONS AND FUTURE DIRECTIONS	94
5.4. CONCLUSIONS	96
REFERENCES	100

1. Introduction

Numbers permeate every aspect of our lives. Over the course of a typical day, we perceive and manipulate numerical information every time we glance at a clock (e.g., “11:30”), when we speak to friends about the outcome of last night’s sporting event (e.g., “our team won by two points”), or in our attempt to choose the shortest (i.e., least populated) queue when buying our morning coffee. From the mundanity of finding our assigned seat on the train that takes us to work (e.g., car 2, row 5, seat 1), to the extraordinary and uniquely human ability for mathematical calculations that allow our species to travel beyond the earth, numerical information ranges from the basic and perceptually unavoidable to complex applications in scientific fields foreign to most of us. This sheer breadth of functions associated with numerical information begs the question: are the approximate representations of numerical quantity, as used when choosing the shortest queue, the same instantiation of number as the digits we use when solving “ $2 + 2$ ”? Does a collection of dots, say ●●●, carry the same meaning as the Arabic digit “3” or the verbal utterance “three”? If so, how do we learn to associate culturally constructed symbolic representations of number, such as “three” and “3”, with the property of “threeness” inherent to the three coins found in our wallets? This thesis aims to further our understanding of these basic aspects of numerical cognition, or the study of the psychological and neurocognitive mechanisms required to perceive and manipulate numerical information.

Although the issue of whether and how different numerical representations share common semantic and neurocognitive bases may come across as mainly philosophical—and is indeed heavily debated in such terms (e.g., Carey, 2004)—it is also crucial to understanding human numeracy in a broader sense. In today’s information-driven age, arguably more so than ever, basic numerical competencies are essential to all aspects of daily life. From being able to properly budget our personal finances, to an increased demand on numerical ability in the workplace (e.g., quantitative data analysis, programming, IT), numeracy is

becoming an increasingly important basic skill on par with the necessity for basic literacy. Despite the importance of such abilities, one in five high-school-aged students in the European Union demonstrate low mathematical achievement and numeracy scores (Eurydice, 2011), detrimental to personal mental health and future employment success (e.g., Parsons & Bynner, 2005). It has further been estimated that approximately 3-7 percent of the school-aged population suffer from *developmental dyscalculia*, a deficit specific to numerical abilities in otherwise typically developing individuals (e.g., Rubinsten & Henik, 2009; Butterworth, Varma, & Laurillard, 2011). Considering this outlook, it is important to reflect on the following: what is it that “goes right” in the four out of five high-school-aged students who possess adequate numerical abilities, or in the approximately 93-97 percent of school-aged children who do not suffer from developmental dyscalculia? In other words, determining what constitutes a deficit (e.g., deviation from a given “mean performance”) requires us to clearly define a baseline grounded in the successful acquisition and deployment of basic number concepts. The overarching aim of this thesis is to begin laying the groundwork for such a baseline, where I begin the process of establishing neurocognitive biomarkers of numerical cognition over the course of typical development.

Understanding how the brain processes basic representations of number is crucial for constraining theoretical, behavioral, and computational models of numerical cognition. Kosslyn and Intriligator (1992) clearly outline such a rationale for cognitive neuroscience in arguing that theoretical descriptions of cognitive processes, as a “function of the brain”, need to align with “neurological reality” (p. 101). That is, theoretical accounts of how the brain represents and manipulates numerical information are best served—and validated—by virtue of their alignment with observed patterns of neural activity. Capturing the essence of this point, seventeenth century philosopher and mathematician Blaise Pascal argued for the instinctual knowledge of first principles, in which he included the domains of space, time, number, and motion (cf. Dehaene, 2011). Some four-hundred years later, evidence from cognitive psychology and neuroscience has

helped validate Pascal’s observations: not only do humans and non-human animals appear to be born with an intuitive sense of number—leveraging similar neural mechanisms across species (e.g., Nieder, 2012)—but the domains of space, time, and number also appear to depend on a generalized neurocognitive system for the processing of magnitude (e.g., Walsh, 2003; Skagerlund, Karlsson, & Träff, 2016). In other words, the instinctual first principles knowledge described by Pascal aligns with neurological reality, suggesting that our use of numbers is an evolutionarily selected and fundamental function of the brain. Even in the absence of tasks requiring participants to act on visually presented number stimuli, neuroimaging data suggests that we cannot help but spontaneously compare and discriminate numerosity (e.g., Piazza et al., 2004; Holloway et al., 2013). I argue that, if number is a fundamental property of the brain, theories of numerical cognition must fundamentally account for how the brain processes number.

1.1. The number sense and nonsymbolic number

Numerical cognition is arguably a *biologically primary ability*, akin to children’s spontaneous acquisition and deployment of verbal language across cultural contexts (e.g., Geary, 2007). Our ability to perceive differences in relative numerical magnitude, for instance by merely observing that two marbles amount to less than four marbles, suggests that the capacity to perceive and manipulate numerosity is an evolutionarily selected, core-cognitive capacity (e.g., Feigenson, Dehaene, & Spelke, 2004). Manifest behaviors in non-human animals and human infants alike support the notion of a basic, language-independent “number sense” among the other senses selected over the course of evolution. For instance, red-backed salamanders consistently choose to hunt gatherings of three as opposed to two fruit flies, indicating a strategically advantageous “preference for more” in a forced-choice experimental paradigm (Uller et al., 2003). Beyond the confines of the laboratory, semi-free-ranging and untrained rhesus monkeys similarly choose to approach more bountiful sources of food, following the observation of human experimenters’ placement of apple slices in

opaque containers (Hauser, Carey, & Hauser, 2000). In both cases, however, this preference for more appears to break down as a seemingly universal limit of three to four objects is exceeded. Once passed, successfully choosing a numerically greater alternative drops to chance levels, indicating a shift from exact to inexact representations of quantity. This limit, commonly referred to as the *subitizing range* (Kaufman, Lord, Reese, & Volkmann, 1949), is also consistently observed when humans perform numerical discrimination tasks (e.g., Gallistel & Gelman, 1992). Subitization differs from mere estimation, as the latter is approximate and takes place—with diminished accuracy—in numerical values above four, whereas the rapid enumeration of up to four objects is typically exact and without error. This suggests that our basic, evolutionarily hardwired numerical processing abilities are on the one hand universally shared with other species, and on the other hand also universally limited to a narrow range of numerical values. The distinction between exact enumeration in the subitizing range and inaccurate, approximate representations of differences in numerical magnitude has led to the proposal of two distinct core systems of number processing (e.g., Feigenson, Dehaene, & Spelke, 2004).

1.1.1. The object tracking system

The object tracking system (OTS) allows for the individuation and accurate tracking of a smaller number of perceived objects and is, as such, often referred to as the *small exact system* (e.g., Gilmore, Göbel, & Inglis, 2018). Prior research indicates that preverbal infants, as young as five months of age, are sensitive to violations of expected arithmetic outcomes within the subitizing range (Wynn, 1992). Using a habituation looking-time paradigm, where longer observations imply novelty or surprise, children observed as either one or two items were placed in a display case. Subsequently, a screen covering the object(s) was raised, occluding them from view. At this point, the experimenter either added or removed an object from behind the screen, clearly showing that either an addition or subtraction of objects was taking place within the case. In some instances, the arithmetic operation was reversed out of sight, producing an impossible outcome (e.g., $1 + 1 = 1$ or $2 - 1 = 2$). As the screen dropped, infants were

found to look significantly longer if the number of remaining items violated the numerical change implied by the observed addition or subtraction of objects. Thus, the OTS appears to allow for preverbal and exact representations of small numbers, as well as basic arithmetic abilities. Neuroimaging data indicate distinct patterns of neural activity during the observation of small and large numbers of objects in six-month-old infants (Hyde & Spelke, 2011), indicative of separate processing systems for numerosities within and beyond the subitizing range.

1.1.2. The approximate number system

Whereas the OTS is governed by a fixed cardinal upper limit of 3–4 objects, the acuity of the approximate number system (ANS)—supplanting the OTS beyond the subitizing range—depends on developmental *distance* and *ratio* effects. Dealing with larger numerosities in an inexact manner, the ANS is also referred to as the *large approximate system* (Gilmore et al., 2018). While the exact representation of, for instance, ●●●●●● as seven dots requires explicit counting, the ANS allows us to estimate that the same collection of dots is likely somewhere within the range of 5–10 objects. Dot arrays are part and parcel of research on number processing abilities, indicative of interesting developmental tendencies that inform numerical cognition more broadly. The simultaneous presentation of two dot arrays is commonly used in numerical discrimination tasks, in order to investigate the limits of both human (e.g., Halberda, Mazocco, & Feigenson, 2008) and non-human (e.g., Agrillo et al., 2012) number estimation ability. Newborn humans prove unable to reliably discriminate numerical dot arrays with ratios smaller than 1:2 (i.e., where one array contains double or half the number of dots), but rapidly develop to successfully discriminate a smaller ratio of 2:3 objects around ten months of age (e.g., Xu & Spelke, 2000). This developmental ratio effect indicates that our approximate representations of numerical quantity become increasingly fine-grained with age. For reference, typically developed adults can discriminate a numerosity ratio of approximately 9:10 (e.g., Halberda & Feigenson, 2008). As a consequence, it has been suggested

that numerosity is represented along a *mental number line* (MNL) that shifts from a compressed logarithmic to an increasingly—but not fully—linear spacing over developmental time (e.g., Dehaene, Dupoux, & Mehler, 1990). This implies the metaphor of a horizontal number line, similar to the X-axis of common graphs, where indices demarcate perceived numerosities. While a smaller number of objects within the subitizing range are represented as equidistant and independent points along this axis, larger numbers are represented as increasingly overlapping points. Practically, this suggests that an array of 15 dots would be represented as a quantity in the approximate vicinity of 15, overlapping with the mental representations of—for instance—13 and 18. This conception is, fittingly, consistent with behavioral characteristics of young children: when asked to draw a number line, greater numbers are typically compressed whereas the spacing of smaller numbers remains linear and equidistant (cf. Rouder & Geary, 2014).

For completeness, it should be noted that the mental number line has also been conceptualized as linear but with “scalar variability” (e.g., Brannon & Merritt, 2011; Dietrich, Huber, & Nuerk, 2015). Although both the logarithmic and linear variations are argued to result in the same behavioral ratio effect (Brannon & Merritt, 2011), the linear model posits this phenomenon as dependent on increased inherent noisiness (i.e., error variance) in larger numerical magnitudes. That is, numerosities are represented as equidistant points on the mental number line but become more difficult to distinguish with increased magnitude. The logarithmic or linear nature of the number line is still a matter of debate, although the former account has traditionally been favored (cf. Siegler & Booth, 2004; Moeller et al., 2009).

1.1.3. Connecting the dots: the MNL, ANS, and IPS

The predominantly logarithmic nature of the mental number line gives rise to the *distance* and *size effects* (Moyer & Landauer, 1967). Following the number line metaphor, two adjacent points on this line are more difficult to distinguish than two independent points separated by a greater horizontal distance along

the axis. The same pattern holds for numerical comparisons: recognizing that ●●● (3) is less than ●●●●●● (7) is easier than discriminating between ●●●●●● and ●●●●●● (7 and 8 respectively). Difficulty, in this context, relates to the psychophysical measures of response time and accuracy. Hence, a more difficult instance of numerical discrimination entails significantly longer response times coupled with decreased accuracy. The size of the numerosities being compared also influences decision-making ability, despite identical distances between two numbers, such that ●●●●●● versus ●●●●●● (9 versus 8) is more difficult to discriminate than ●●●● versus ●●●● (4 versus 5).

These performance patterns are expressed in the form of a *Weber fraction*, following the Weber-Fechner law of “just noticeable differences” in perceived magnitude (e.g., Dehaene, 2003) and commonly used as a measure of individual ANS acuity (e.g., Halberda et al., 2008). In other words, the Weber fraction (w) can be understood to indicate how precisely an individual is able to represent numerical magnitude, as informed by correctly noticed differences between dot arrays across different comparison ratios (e.g., Starr, Libertus, & Brannon, 2013). A smaller w thus indicates the ability to discriminate between smaller ratios. The typical twenty-year-old adult with an average w of 0.11 can correctly discriminate a ratio of 9:10 objects, whereas three-year-old children, with a w of approximately 0.53, are limited to ratios of 2:3 (Halberda & Feigenson, 2008).

The neurobiologically grounded existence of a mental number line is supported by neuroimaging evidence in both humans and non-human primate subjects (e.g., Dehaene & Cohen, 1997; Dehaene et al., 2003; Nieder & Miller, 2004; Roitman, Brannon, & Platt, 2007). In humans, the *intraparietal sulcus* (IPS) is consistently activated during nonsymbolic number discrimination tasks (e.g., Piazza et al., 2004; Ansari & Dhital, 2006; Lyons & Ansari, 2009; Holloway, Price, & Ansari, 2010). The strength of this activity is modulated by numerical

ratio (e.g., Holloway & Ansari, 2010), such that near-distance number comparisons elicit greater activity—presumably as a function of effort associated with discriminating adjacent numerosities on the MNL—than far-distance comparisons. The IPS is also active during the mere presentation of numerical stimuli, in the absence of task or response demands, suggesting that this neural activation occurs as a function of perceiving numerosity rather than as a function of explicit comparison demands (e.g., Piazza et al., 2004). Even in the absence of prior number discrimination training in rhesus monkeys, similar neural activation patterns have been observed in the IPS-homologous (i.e., functionally equivalent) ventral intraparietal area (e.g., Nieder, 2011) as well as the dorsolateral prefrontal cortex (Viswanathan & Nieder, 2013). Such results are interesting for at least two reasons: first, equivalency of neural responses may be indicative of the evolutionarily inherited nature of the ANS and MNL. The use of single-cell recordings in individual neurons, as afforded by non-human primate studies, allow for greater spatial resolution than typical neuroimaging methods employed for human participants. Using this method, Viswanathan and Nieder (2013) found that individual neurons were numerosity-selective within (i.e., less than 3–4 objects) and beyond (i.e., 5 and above objects) the subitizing range, indicating discrete representations of specific numerosities at the neuronal level. Second, the pattern of activity distributed across the posterior parietal and prefrontal cortices aligns well with recent proposals of a human frontoparietal network of neural regions implicated in numerical cognition (e.g., Sokolowski, Fias, Mousa, & Ansari, 2016).

1.2. The symbolic reference gap and symbolic number

Thus far, this overview of number processing abilities and the systems that govern them has focused exclusively on the perception of concrete objects and (e.g., physiological) sensations. Such instances of nonsymbolic number relate to situations where we divide marbles among friends, hear the nine piano notes constituting the main motif of Beethoven’s *Für Elise*, or when we feel the two distinct haptic taps produced by our phones as a text message arrives. Returning to

the simile between numerical cognition and language abilities, a glaring issue of the biological primacy account becomes apparent: how do we account for sociocultural inventions that apply these basic cognitive capacities in novel ways, which cannot have been selected by evolution? While verbal language spontaneously develops across cultural contexts, the biologically secondary abilities of reading and writing do not (e.g., Geary, 2007). Likewise, applied uses of symbolically represented number (e.g., “2” or “two”) in areas such as trade, arithmetic, and statistics requires cultural adaptation through education, language, and socialization (cf. Butterworth, Reeve, and Reynolds, 2011; Dehaene & Cohen, 2007; Núñez, 2017).

This apparent rub between preverbal, nonsymbolic representations of number and their symbol-based instantiations has led to the explicit differentiation of nonsymbolic and symbolic number processing abilities. Núñez (2017) takes this even further when appealing to the *symbolic reference gap*, arguing that the terminology surrounding “number” should be reserved for symbol-based quantifiers that—among other—possess cardinality (i.e., countability), ordinality (i.e., sequential positional value in the count-list), and constitute exact references to a given numerosity. The nonsymbolic number processing capacities shared with animals should, in Núñez’s view, rather be termed *quantical* abilities that may at best serve as “biologically evolved preconditions” (p. 419) for (symbolic) numerical capacities.

The issue of whether nonsymbolic and symbolic numbers are processed by the same underlying cognitive mechanism, altogether different ones, or overlapping but separable mechanisms is still a matter of active debate (e.g., Leibovich & Ansari, 2016; Reynvoet & Sasanguie, 2016). While there appears to be a consensus regarding the biologically hardwired nature of nonsymbolic number (i.e., quantity) processing in the small exact (OTS) and large approximate (ANS) systems, two main competing explanations exist for the acquisition and deployment of symbolic numbers. These can be termed the “OTS bootstrapping” and “ANS alone” (i.e., ANS bootstrapping) accounts (Le Corre & Carey, 2007).

1.2.1. OTS bootstrapping

The OTS bootstrapping account argues that our ability to precisely represent small quantities is sufficient for establishing semantic reference between perceived numerosity and associated number symbols in the subitizing range (e.g., Carey, 2004; Le Corre & Carey, 2007). This process is argued to entail the mapping between the number of objects represented in visuospatial working memory and the—at first—semantically deficient count-list (i.e., “one, two, three, four”). That is, as children first start uttering the verbal count-list, an association is made between the number of visually (or e.g., auditorily) perceived concurrent objects as represented by the OTS, which are in turn instantiated as mental symbols for each object in the subitizing range (cf. Hyde, 2011). Carey (2004) has argued that children thereafter make use of a bootstrapping process to infer that “five” has a cardinal value of exactly “one more” than “four”, which eventually scales up to cover increasingly larger cardinal values. As I understand this position, it does not necessarily prohibit a period over the course of development where children also utilize approximate representations of larger quantities. For instance, when an experimental manipulation may prohibit explicit counting, it is plausible that analog magnitudes serve to provide an approximate answer mapped onto a symbol (e.g., ten dots may be estimated to correspond to the symbol “9”).

1.2.2. ANS bootstrapping

Approximately five-year-old children begin to exhibit the same numerical distance effect, observed for nonsymbolic number discrimination, in symbolic tasks employing Arabic digits (e.g., 3 versus 4; Le Corre & Carey, 2007). This is commonly argued, at a minimum, to indicate a common underlying processing strategy across different numerical formats. Taken further, such similarities have been used to argue that number symbols gain their meaning by explicit mapping against the ANS (cf. Dehaene, 1992; Opfer, Thompson, & Kim, 2016). This position suggests that the ANS, alone, constitutes the semantic basis for

our understanding of numbers. As nonsymbolic numerical magnitudes are perceived and mapped against the mental number line, numerical reference points are established, which can then be leveraged to map and represent the value of number symbols. A child who visually perceives five toys while their parent concurrently utters the word “five” therefore establishes semantic reference between the analog numerosity (●●●●●) and its associated symbolic representation (“five”), by virtue of associating both to the same position on the mental number line. In this sense, the ANS can be argued to scaffold the development of symbolic number processing (cf. Odic & Starr, 2018).

This position has received considerable support, indicative of a relationship between ANS acuity and symbolic math achievement. Even when measured at six months of age, discriminatory performance of the ANS (controlled for general intelligence) has been observed to robustly predict standardized math scores three years later (Starr, Libertus, & Brannon, 2013). This pattern furthermore holds over developmental time, indicating that preschool-aged children’s and college-aged students’ symbolic arithmetic abilities improve after practicing approximate (i.e., dot array-based) arithmetic tasks (Park et al., 2016). Notably, this outcome does not appear to apply in the opposite direction, as practicing symbolic arithmetic has not been observed to increase ANS acuity (Lindskog, Winman, & Poom, 2016). Such a unidirectional pattern may be taken to suggest a need for mapping symbolic numbers against the ANS, in line with the idea that the ANS constitutes our primary semantic representation of number (cf. Dehaene, 1992). This could be compared to language abilities: learning a foreign language is dependent on the same basic mechanisms as used for one’s native language (e.g., syntax, grammar), but increased fluency in a foreign language does not automatically improve native-language proficiency. Put differently, this may entail that manipulation of numerical stimuli in their “native” approximate analog magnitude form results in the ability to distinguish smaller numerical distances, which decompresses the mental number line and allows for more precise representations of symbolic number.

1.2.3. Mixed evidence for ANS bootstrapping

At the neurocognitive level, studies have shown mixed evidence for the ANS bootstrapping account of symbolic number acquisition and processing. While studies in adult participants have indicated a shared reliance on the IPS during both nonsymbolic and symbolic number processing (e.g., Cantlon et al., 2006; Izard et al., 2008), suggesting the mapping of number symbols onto the ANS (cf. De Smedt et al., 2013), studies featuring children are indicative of considerable developmental differences. Common to both children (e.g., Ansari et al., 2005; Libertus, Brannon, & Pelphey, 2009) and rhesus monkeys (e.g., Diester & Nieder, 2007), symbolic number processing has been observed to elicit significantly more activity in the prefrontal cortex than IPS when compared to human adults. It has been hypothesized that symbolic number processing “migrates” from the prefrontal to parietal cortex over the course of development, as a result of increased symbol-mapping proficiency (e.g., Ansari et al., 2005). Consistently observed prefrontal activity (particularly in the ventrolateral PFC) in human children and non-human primates may therefore indicate an increased reliance on domain-general cognitive mechanisms, such as cognitive control and working memory, recruited to compensate for a lack of experience with symbolic representations and their semantic content. These findings align with the *developmental calculation model* (Kaufmann, Wood, Rubinsten, & Henik, 2011), arguing that nonsymbolic and symbolic number begin as distinct and notation-dependent representations, as evidenced by distinct patterns of neural activity both across numerical representational formats as well as over developmental time. Over the course of aging, education, and the development of domain-general abilities (e.g., visuospatial attention, working memory, and language), these disparate representations are argued to become increasingly integrated. This integration may allow for format-independent and abstract processing of numerical information in the IPS, as supported by a mapping of numerical stimuli against the ANS (cf. De Smedt et al., 2013).

The relationship between ANS acuity and mathematics proficiency gives credence to the view that symbolic number is acquired and deployed through a mapping against the ANS, rendering nonsymbolic magnitude as the primary semantic representation of number (e.g., Dehaene, 1992). However, recent studies increasingly question the strength of this relationship, indicating that individual differences in symbolic arithmetic abilities are more appropriately explained by symbolic number processing abilities (e.g., Leibovich & Ansari, 2016; Krajcsi, Lengyel, & Kojouharova, 2018). Accordingly, such results question whether the predisposed and approximate capacity for perceiving quantity is sufficient for establishing semantic reference, or if additional domain-general cognitive mechanisms are required to give number symbols their semantic content.

1.3. Cognitive domain-specificity and domain-generality

In order to fully discuss the domain-specificity and domain-generality of cognitive abilities, a clarification of these terms is in order. Cognitive domain-specificity refers to distinct—and often evolutionarily predisposed—abilities that apply exclusively to one particular domain and are often not meaningfully fractionated into smaller constituent parts. They may, however, act as “input modules” to higher-order cognitive processes. A typical example of cognitive domain-specificity is *visual face processing*, which is a basic cognitive ability supported by the brain’s *fusiform face area* in at least humans (e.g., Dehaene-Lambertz et al., 2018) and macaque monkeys (e.g., Tsao et al., 2006). While this ability could theoretically be fractionated into increasingly more basic abilities (e.g., distinguishing orientation, color, and geometry in the early visual cortex), the processing of faces is—*prima facie*—a conceptually meaningful ability that serves a basic socio-cognitive need: distinguishing friends from foes without the need for additional sensory input from other domains (e.g., hearing). However, the domain-specific cognitive processing of a visually perceived face may act as input to higher-order cognition, such as relating an individual’s face to the declarative knowledge of their name, or the recollection of episodic memories—for instance of the party at which we first met them. Domain-generality refers to cognitive

processes that act in a more universal fashion and exert their influence over an individual's cognition as a whole, such as one's level of nonverbal intelligence or working memory capacity. That is, regardless of the domain a given task is performed in (e.g., mathematical, linguistic, or spatial), domain-general cognitive abilities serve to impose similar constraints and benefits on performance. Language is arguably a domain-general cognitive ability, as it supports the acquisition of knowledge across multiple domains and may itself be supported by a general statistical learning mechanism (e.g., learning syntax as a function of experiencing naturalistic occurrences of language; cf. Ambridge, Pine, & Lieven, 2014). As an example, insufficient spatial language acquisition has been observed to negatively influence performance on spatial search tasks, suggesting that language is an important prerequisite for spatial cognition (Pyers et al., 2010). It can thus be argued that language provides a domain-general framework that allows for higher-order cognitive abilities (e.g., Gentner, 2016).

An increasing number of studies have begun to converge on a model of symbolic number processing based primarily on executive function and memory capacities, rather than the mapping of corresponding approximate numerical magnitude. In a study of mathematical performance in 9-year-old children, none of the standard ANS measures (e.g., dot comparison, number comparison, rapid number naming in the subitizing range) predicted mathematical achievement (Szucs, Devine, Soltesz, Nobes, & Gabriel, 2013). The authors rather found that mathematical achievement was only reliably predicted by measures of verbal (intelligence and phonological ability), visual (short-term and working memory), spatial (mental rotation, symmetry, and orientation), and executive function (inhibition and task-switching). While formal arithmetic and symbolic number discrimination constitute separate tasks, given the importance of—among others—procedural knowledge and access to rote verbal representations (employed primarily in multiplication; Lee & Kang, 2002), symbolic number comparison demonstrated a stronger correlation with mathematical achievement than approximate and nonsymbolic number comparison. These results

suggest that the domain-general mechanisms inherent to mathematics also extensively apply to basic symbolic number processing, which questions whether the ANS needs to be recruited for symbolic number processing.

1.3.1. The overlapping nature of magnitude processing

Walsh's (2003) *a theory of magnitude* (ATOM) argues that the brain is genetically predisposed with a generalized magnitude system, covering the perceptual dimensions of time and space in addition to number. These three dimensions are argued to be inseparable qualities of any perceptual experience, as everything we experience is represented at a point in time, a position in space, and inherently features numerosity. Thus, the evolution of a domain-specific magnitude system would make evolutionary sense, for instance when avoiding a number of predators situated at a certain distance and therefore a certain time away from the potential prey. It is also plausible from the perspective of perception and the performance of motor actions to interact with the surrounding world, as all motor actions are governed by these three domains.

Empirical evidence for such an association is found, for instance, in the spatial-numerical, spatial-temporal, and temporal-numerical associations of response code (SNARC, STEARC, and TiNARC, respectively). The SNARC effect indicates—in line with the MNL—that numerosity is mentally represented as ascending from left to right, which is demonstrated by faster and more accurate decisions when the larger number is placed to the right in a number discrimination task (Dehaene, Bossini, & Giraux, 1993). Conversely, when the larger number is placed to the left, reaction times are slower and responses less accurate, suggesting an interference effect between spatial and numerical representations. Similar Stroop-based interference has also been observed for the physical size of numerical stimuli, where increases in font size congruent with the larger number (i.e., when the numerically larger digit is also physically larger) promote faster and more accurate decisions (e.g., Cohen Kadosh, Bien, & Sack, 2012). The STEARC effect likewise demonstrates an association between the perceived tim-

ing of auditory cues and the lateralization of keyboard responses, where perceived early onsets of a cued auditory stimulus promoted faster responses with a leftward key (e.g., Ishihara, Keller, Rossetti, & Prinz, 2008). Later onsets were responded to faster with a rightward key, suggesting that the temporal dimension also benefits from a spatial mental representation (*mental time line*) increasing to the right. Finally, the TiNARC effect (e.g., Fabbri, Cancellieri, & Natale, 2012) demonstrates an interaction between time and number, such that performance on a time bisection task (i.e., where participants are asked to determine whether a temporal duration is short or long) is modulated by a numerical cue. For instance, Vicario (2007) found that participants judged the presentation of small numerosities (e.g., 1) as shorter than a reference stimulus of 5 (presented for 300 ms), and large numerosities (e.g., 9) as lasting significantly longer than the reference.

This pattern of interactions provides a compelling argument for the existence of a native, or genetically predisposed, generalized magnitude system for space, time, and number. Such an account would also be consistent with research in developmental psychology, demonstrating that young children find it difficult to separate these three domains until at least the end of the preoperational stage of development (taking place approximately between the ages of 2 and 7). Piaget (1953) noted that young children are usually unable to distinguish size from numerosity, often conflating more spatially extended—for instance in terms of being spread out—collections of objects (e.g., marbles) with absolute numerosity. These results are consistent with the intuitive *more A—more B* rule, arguing that increases in one domain transfer to another domain (Stavy & Tirosh, 2000). Specifically, children in Piaget’s sensorimotor and preoperational stages regard spatially but not voluminously larger containers to hold more liquid, and often assume that larger cars travel faster than smaller cars—regardless of access to conflicting information. I argue that these behaviors are indicative of a difficulty in separating the domains of time, space, and number, which are tightly knit in nature and provide a simple—but fallible—heuristic for interaction with the outside world. In line with this proposition, there is reason to believe that number

itself is not special or strongly domain-specific, in the sense that a capacity specific to number processing has been evolutionarily selected for, but rather that educational and cultural practices promote the dissociation of number from other magnitudes as especially relevant. This position is consistent with neuroimaging data, demonstrating an overlap of neural correlates for spatial, numerical, and temporal discrimination tasks: bilateral inferior frontal gyrus (IFG), bilateral insula, right middle frontal gyrus (MFG), intraparietal sulcus (IPS), supplementary motor area (SMA), middle orbital gyrus (MOG), and premotor cortex (PMC; Skagerlund, Karlsson, & Träff, 2016).

1.3.2. Executive functions influence number processing

A hypothesis targeting the development of executive function as central to the separation of space, time, and number, as well as to the development of numerical cognition, is consistent with results implicating deficient executive function as one of the primary causes of developmental dyscalculia (Ashkenazi & Henik, 2010). The authors demonstrate that, in the absence of attention deficit hyperactivity disorder (ADHD), domain-general attention deficits impede the retrieval of arithmetic facts, conflict resolution, and inhibition of irrelevant responses. Minimally, the latter two factors are plausibly important for the separation of number from irrelevant perceptual cues (e.g., surface area, dot color, font size). These results are also consistent with evidence suggesting increased activity in the medial frontal gyrus, inferior frontal gyrus, precentral gyrus, and insula in children during the performance of number discrimination tasks, compared to the developmental shift towards stronger reliance on the parietal lobes in adulthood (Ansari et al., 2005). Functional hyperconnectivity between parietal and frontal regions in children with developmental dyscalculia has additionally been observed to diminish following number line training (Michels, O’Gorman, & Kucian, 2018), a task which has been argued to target proportional reasoning due to the interaction of spatial and numerical ratio information (e.g., Boyer, Levine, & Huttenlocher, 2008). Proportional reasoning is dependent on the construction and execution of a task within a well-defined problem space,

and number line training may be a means of reducing the load on executive functions by highlighting the interaction of space and number as to define the problem space for further number processing tasks (cf. Babai, Cohen, & Stavy, 2018).

1.3.3. Separable systems of number processing?

Lyons, Ansari, and Beilock (2012) experimentally evaluated the relationship between the ANS and symbolic number discrimination using a mixed-format condition, where participants were asked to select the numerically larger alternative represented as a dot array or Arabic digit. If it were the case that numerical symbols map onto approximate representations of quantity, the authors suggested that reaction times and response accuracies should be similar for within-format (i.e., two Arabic digits or two dot arrays) comparisons and mixed comparisons. The mixed-format condition was observed to be significantly more difficult than the within-format condition, and additionally proved to be more difficult than the mixed comparison of two symbolic numerical formats: Arabic digits and number words (e.g., “5 or four”). These results are further strengthened by the finding that young children display an asymmetry of mapping performance between dot arrays and number words, such that they can effortlessly tap a sequence corresponding to a number word (e.g., five taps following the word “five”) but had difficulty describing a number of dots or taps with number words (Odic, Le Corre, & Halberda, 2015). Together, these studies indicate the existence of two separate systems of numerical cognition, where one targets the approximate estimation of quantity (i.e., a generalized magnitude system used to evaluate the perceptible difference of more or less *stuff*; cf. Buetti & Walsh, 2009), and a system for semantic binding and retrieval of numerical facts in memory. As such, the ANS may not be “about” (i.e., specific to) numerosity as much as it enables the perception of differences in relative magnitude—whether in intensity of light and sound, or visually perceived groups of objects (cf. Núñez, 2017). The symbolic number system, in comparison, has been argued to combine the exact enumeration of objects in the subitizing range (1–4) with the

counting sequence (e.g., Le Corre & Carey, 2007), resulting in an abstract semantic understanding of a symbolic number as some amount more numerous than a preceding number.

The conflicting nature of results, both at the behavioral and neurocognitive levels, suggests that the debate of how symbolic numbers acquire their semantic content is far from settled. Is there a domain-specific cognitive capacity for number, inherited by evolution, that is leveraged to give meaning to culturally constructed number symbols? May it rather be the case that symbolic number is processed independently of approximate nonsymbolic number, but that both leverage foundational domain-general cognitive capacities—such as executive functions and visuospatial attention—and therefore appear behaviorally correlated? In order to empirically evaluate these questions, the purpose of this thesis is to compare the neurocognitive foundations and developmental aspects of number processing across the three naturalistic representations of number encountered in everyday life: Arabic digits (e.g., “1”), number words (e.g., “two”), and analog representations of nonsymbolic numerical magnitude (e.g., ●●●).

1.4. The triple code model

One of the central theoretical models in the field of numerical cognition, as well as the principal impetus for this thesis, is Dehaene’s (1992) *triple code model* (TCM). While prior models had generally relied on symbol-based number processing abilities (e.g., calculation) to describe the cognitive mechanisms underlying syntactic perception and manipulation of numerical information, the semantic acquisition of number concepts had received less attention. In other words, the primary aim of the TCM is to provide an explanation for how number symbols acquire their meaning from our evolutionarily inherited capacity for approximate numerosity estimation and subitization. To this end, Dehaene posited the existence of three naturalistic mental representational codes for number: the analog magnitude representation, the visual Arabic number form, and

the auditory verbal word frame. Although the assumptions of the TCM have already been tacitly discussed throughout this introductory chapter, what follows is a more principled examination of how the model accounts for the link between nonsymbolic and symbolic representations of number.

1.4.1. The primacy of analog magnitude

At its core, the TCM argues that the capacity for analog numerical magnitude representation begets symbolic representations of number, serving as the foundation for subsequent complex applications such as arithmetic. The three codes interface with one another, such that an Arabic digit (e.g., “6”) may be asemantically translated to its corresponding verbal label (e.g., “six”), but this process is crucially mediated by a semantic mapping against the analog magnitude representation (e.g., ●●●●●) governed by the ANS and MNL. Therefore, the magnitude code is argued to be the “main, and perhaps the only, ‘semantic’ representation of numbers” (Dehaene, 1992, p. 35). Deficit studies corroborate such a view, as evidenced by the frequent occurrence of intact nonsymbolic numerical magnitude processing abilities when impairments debilitate processing in either the visual Arabic (e.g., Cipolotti, Warrington, & Butterworth, 1995), verbal (e.g., Jefferies, Bateman, & Lambon Ralph, 2005)—or even both (cf. Dehaene, 2011)—representational codes.

The hypothesized neural basis of the TCM indicates the primacy of the core-cognitive approximate number system for numerical cognition (Dehaene & Cohen, 1995; Dehaene & Cohen, 1997; Dehaene et al., 2003). It is argued that the consistent activation of the intraparietal sulcus “whenever numbers are manipulated, independently of number notation, and with increasing activation as the task puts greater emphasis on quantity processing” (Dehaene et al., 2003, p. 487) designates it as the central domain-specific neural correlate of numerical cognition. As a result, the IPS processes number regardless of the code in which it is represented, by virtue of mapping representations against the mental number line to establish semantic reference. It is in other words argued to be the case

that number discrimination tasks in both the Arabic, verbal, and nonsymbolic magnitude codes jointly depend on the IPS.

1.4.2. Symbolic number and semantic reference

Symbolic number processing extends the need for domain-general cognitive resources, due to its culturally constructed nature (cf. Dehaene & Cohen, 2007). Verbal representations of number require the recruitment of left hemisphere language regions of the brain—known as the *perisylvian language network*—in order to perceive and manipulate number syntax, phonology, orthography, verbal arithmetic facts, and so forth. Early conceptions of the TCM (Dehaene & Cohen, 1995) argued for the principal involvement of the “classical language areas” (p. 88), constituting the inferior frontal gyrus (IFG), superior and middle temporal gyri (STG and MTG), as well as thalamus and basal ganglia. A later account (Dehaene & Cohen, 1997) also differentiated between direct and indirect routes of verbal number processing. The direct route applies to arithmetic processing, utilizing the left cortico-subcortical loop to map visual and verbal perceptual input to rote, asemantic memories of arithmetic facts (e.g., $6 \times 6 = 36$). In contrast, and more applicable to the TCM, the indirect route leverages left-hemisphere language regions to mentally represent verbal perceptual input (e.g., “two”) and recruits the IPS to encode it as a semantic representation of numerical magnitude (e.g., ●●) in the absence of rote verbal knowledge. This route is particularly relevant to numerical discrimination, given that such tasks require explicit comparisons of relative numerical magnitude (e.g., “two” versus “three”) and do not afford overlearned, asemantic mental representations as found in arithmetic. That is, with sufficient practice one can immediately “see” that $2 + 2$ equals 4 without particularly reflecting on why this is the case, whereas explicit comparisons of numerical magnitude require a semantic understanding of the operands (i.e., [“two” = ●●] < [“three” = ●●●]).

Arabic digit processing depends principally on the successful visual recognition of culturally meaningful line segments in the ventral occipital-temporal cortex.

Dehaene and Cohen (1995) did not explicitly localize this neural correlate to either hemisphere, but later research has predominantly positioned this so-called *visual number form area* in the right inferior temporal gyrus (ITG; cf. Yeo, Wilkey, & Price, 2017). A similar but left-lateralized region for the visual processing of written words has been identified in literate adults and children, observed to be substantially less active in individuals who either learned to read in adulthood or are functionally illiterate (cf. Dehaene et al., 2015). This suggests that culturally evolved capacities may, over the course of development, leverage existing low-level perceptual processing abilities and create brain–behavior feedback loops based on experienced stimuli. Moreover, the existence of such a region for reading increases the probability of a functionally equivalent region for digit recognition, as both literacy and numeracy skills are cornerstones of modern society. It is, however, plausible that Arabic digit processing also leverages language regions of the brain, given the developmental primacy of associating number words to numerical quantities before learning their corresponding Arabic digits (e.g., Fayol & Seron, 2005).

In summary, the TCM argues for separate domain-general (e.g., language and vision) but partially overlapping, domain-specific (i.e., numerical magnitude representation) cognitive mechanisms for numerical cognition. Investigating potential overlap in the recruitment of neural correlates and functional neural circuits, across the three number codes, is a fruitful avenue for examining the neurocognitive relationships between different numerical representations. Such an approach may provide foundational empirical evidence of the semantic acquisition of symbolic number, its relationship to nonsymbolic number, and furthermore detail developmental effects that inform our understanding of the cognitive mechanisms children require to become numerically competent adults. It is therefore surprising that, despite the popularity of the TCM in the numerical cognition literature, no prior research has systematically investigated its neurological veracity by concurrently examining all three codes in either children or adults.

1.5. Numerical magnitude and numerical order

Numbers do not only relay an exact cardinal value, such that the Arabic digit “2” is equivalent to the word “two” or two visually perceived marbles, but also inherently feature a sequential positional order-value (i.e., *ordinality*). This duality of number can appropriately be seen in how we use language. Imagine, when planning a large dinner party, asking a few friends to help carry a total of thirty-two chairs. These thirty-two distinct objects are then placed at a table, to which four friends may agree to carry eight chairs each. A seating chart is then drawn up to help alleviate unnecessary confusion. As guests begin to arrive, they consult said chart to determine that their particular seat is the “fourth from the left” or “two seats away from my best friend”. In this scenario, the exact cardinal value of available seats (i.e., 32, or 8 each for 4 carriers) is less important—barring any unforeseen last-minute guests in need of a chair—than their relative position to one another in the count-list. Nevertheless, both of these properties are inherent to number regardless of whether a situation calls for judgment of cardinal or ordinal value. The same principle applies for symbolic numbers, which denote a particular cardinal value (e.g., 2) *and* simultaneously convey the ordinal fact that, say, 2 comes before 3 and after 1 (i.e., $1 < 2 < 3$; cf. Núñez, 2017). Similarly, this use of numerical ordinality applies when finding our assigned seat on a train, where we must first determine how to locate the train car (e.g., car 2 should be after car 1 but before car 3), then find the right row of seats (e.g., row 5 out of 20), before finally arriving at a seat marked with the cardinal referent “1”. Despite such ubiquity of numerical order use in everyday life, the ordinal aspect of number has received considerably less attention from researchers than numerical cardinality (cf. Cohen Kadosh & Dowker, 2015; Lyons, Vogel, & Ansari, 2016).

1.5.1. The case for separate cardinal and ordinal systems

It has been proposed that the numerical properties of ordinality and cardinality are supported by two separate, domain-specific core systems. This hypothesis is based on at least three primary lines of evidence, indicative of dissimilarities in

numerical order and magnitude processing. First, while cardinal numerical magnitude discrimination is subject to similar distance effects regardless of representational format, determining the ordinality of a number sequence (e.g., whether 1-2-3 is correctly ascending) gives rise to a *reversed distance effect* (e.g., Caplan, 2015). That is, when the distance between—for instance—three Arabic digits is small, responses are faster and more accurate than for larger distances (e.g., when determining whether 1-3-5 is correctly ascending). The variability in distance effects between cardinal and ordinal number processing could therefore suggest that these two aspects of number are manipulated in a qualitatively different fashion. Second, ordinal number processing abilities have, compared to cardinal number discrimination abilities, been observed to better predict arithmetic abilities from middle school and onward (e.g., Lyons et al., 2014)—again suggestive of qualitative differences attributable to order and cardinal value. Finally, Rubinsten and Sury (2011) found that numerical deficits can separately impair the cardinal and ordinal processing of number, resulting in a dual-systems model of number processing.

1.5.2. Implications for numerical cognition

Comparing numerical magnitude and order processing may prove to be important for understanding the acquisition of number semantics. While the TCM aligns most clearly with the ANS bootstrapping account, arguing that numbers gain semantic reference through the analog magnitude code supported by the mental number line (e.g., Dehaene, 1992), this view has—as discussed—received considerable criticism (e.g., Leibovich & Ansari, 2016). Proponents of the OTS bootstrapping account (e.g., Carey, 2004) suggest that the establishment of semantic reference between a small number of precisely perceived objects (e.g., four marbles and the referent “four”) and its corresponding symbolic representation suffices to infer that “five” is exactly “one more” than “four”. Consequently, it may be the case that knowing the count-list is enough to semantically grasp the cardinal value of larger numbers, such as 452—which is “one more” than 451, “one less” than 453, and situated approximately between 400 and 500.

If so, number symbols would acquire their semantic content “based on the ordinal information enclosed in the symbol sequence” (De Smedt et al., 2013, p. 51), which may happen to concurrently increase ANS acuity but fundamentally depends on cognitive mechanisms specific to symbol-based processing. Answering the question of whether separate or common cognitive mechanisms govern ordinal and cardinal number processing may thus be informative for answering the broader question of how—and if—a collection of three dots may convey the same meaning as “3” or “three”. Down the line, such knowledge has further implications for designing educational curricula serving to support children’s successful acquisition of basic number concepts, promoting the development of numeracy and arithmetic abilities.

2. Aims

The overarching aim of this thesis is to increase our understanding of how the neurotypical child and adult brain perceives and processes numerical information. The explicit mapping and delineation of neurocognitive correlates associated with basic number discrimination has received limited attention in prior research, particularly for healthy and typically developing participants (cf. Kaufmann, Wood, Rubinsten, & Henik, 2011). As a means of advancing the field of numerical cognition towards establishing generalizable biomarkers of deficient numerical abilities, this thesis seeks to provide a neurotypical baseline against which atypical numerical cognition may be evaluated. While more research remains to be conducted in additional populations across the lifespan, from early childhood to late adulthood, this thesis serves as a steppingstone towards the larger goal of mapping the neurocognitive foundations of typical number processing abilities across the entire lifespan.

Three principal research questions provide a common ground to all papers included in this thesis: how does the brain process different numerical representations? Is this processing dependent on shared neurocognitive mechanisms or attributable to unique, task and format-dependent cognitive processes? What are the effects of biological and cognitive maturation on numerical processing abilities? Beyond these principal questions, specific aims respectively associated with the featured papers follow below.

2.1. Paper I

Despite being one of the central theoretical models foundational to the field of numerical cognition, no study had—prior to Paper I—empirically investigated the neural correlates associated with each of the three codes (i.e., Arabic digits, verbal number words, and nonsymbolic representations of numerical magnitude) described by the TCM. At most, previous empirical research had compared and

contrasted the neural activity patterns associated with the performance of up to two codes (most commonly the Arabic and nonsymbolic representational formats; e.g., Kaufmann et al., 2011). It should be noted that one previous study, by Peters and colleagues (2016), comes closest to examining the neural correlates of the entire model in a sample of child participants. However, the experimental design of this study required participants to perform mental calculations with the presented Arabic, verbal, and nonsymbolic numerical stimuli, arguably adding an additional layer of complexity to the basic discrimination of numerosity. The aim of this paper was therefore to provide an empirical validation of the—primarily theoretically informed—neural correlates outlined by the TCM (e.g., Dehaene & Cohen, 1995). To this end, forty-six typically developed young adult participants were recruited for an fMRI-based neuroimaging study, in order to provide a representational baseline of typical numerical discrimination abilities.

2.2. Paper II

Having examined the neural correlates of typical adult-level numerical discrimination abilities in Paper I, establishing a post-adolescent developmental target state, the aim of Paper II was to investigate the similarities and differences of neural correlates associated with numerical discrimination abilities in children and adults. To this end, thirty typically developing children were recruited for an fMRI-based neuroimaging study. The study was in all respects identical to the one performed in Paper I, in terms of data acquisition (e.g., hardware, MRI protocols) as well as included tasks and experimental design. Given that no prior study had administered tasks related to each of the three numerical codes, nor provided a direct empirical comparison between the neural activity patterns elicited by these tasks during different developmental stages, the main purpose of Paper II was to validate previous meta-analytic research describing the neural correlates of number processing in children (Arsalidou et al., 2018) and adults (Arsalidou & Taylor, 2011).

2.3. Paper III

Cognitive processes are not only reliant on the activity elicited by particular neural regions, but also on the patterns of functional connectivity between micro- and macroscale neural circuits. Recent research in numerical cognition argues for a shift in focus towards these latter functional circuits, with mounting evidence indicating substantial engagement differences in children and adults (cf. Iuculano, Padmanabhan, & Menon, 2018). Finding limited differences in children's and adults' activation of neural regions during numerical discrimination tasks (Paper II), two unresolved questions remained to be answered in Paper III: how do the interactions between functional circuits engaged by children and adults during number discrimination differ, and are these differences modulated by different numerical representational codes as described by the TCM? Potential differences in recruited functional circuits may also be informative to the question of whether symbolic and nonsymbolic numerical cognition leverage similar or distinct processing systems, informing whether number semantics are consistently established through the ANS. To this end, an analysis of the functional connectivity patterns between twenty-two theoretically motivated neural regions of interest (ROI) was performed, comparing and contrasting a sample of fifty-one adults and thirty-seven children.

2.4. Paper IV

At approximately 10–12 years of age, a critical neurodevelopmental maturation period coincides with numerical order processing abilities significantly surpassing numerical magnitude discrimination abilities as the key predictor of arithmetic ability (e.g., Lyons et al., 2014). Recent research has increasingly supported the view of two separable neurocognitive mechanisms (e.g., Rubinsten & Sury, 2011), respectively associated with numerical cardinality (i.e., quantity discrimination) and numerical ordinality (i.e., sequential positional value judgments), in contrast to the traditional view of a singular cardinal number processing mechanism (e.g., Wilson & Dehaene, 2007; Butterworth et al., 2011).

However, the nature and potential dissimilarity of the neural mechanisms supporting numerical order and magnitude processing remains unclear. To this end, Paper IV investigated the neural correlates uniquely recruited by separate numerical order and magnitude discrimination tasks in thirty-seven typically developing children between the ages of 10 and 12. Furthermore, in order to allow for inferences at the level of cognitive mechanisms, a cross-validated brain–behavior correlation approach was used to investigate if whole-brain functional connectivity patterns (i.e., functional connectomes), acquired during task performance, could be leveraged to predict separately administered cognitive-behavioral outcome measures. The purpose was thus to disentangle the contributions of different cognitive abilities (e.g., literacy, working memory) to the two number processing mechanisms, as well as to quantify the extent of their dissimilarity based on predictive patterns elicited by task-based functional connectomes.

3. Methods

The following chapter will provide a brief overview of the participants, methods, and research equipment featured in this thesis. Interested readers are encouraged to read chapter 4 and Papers I–IV for more in-depth descriptions of relevant methodological considerations.

3.1. Participants

A total of ninety-three healthy, right-handed individuals participated in the studies covered by Papers I–IV. Out of this sample, thirty-nine were typically developing children aged 10–12 years. Due to data quality considerations, two participants were fully excluded from further data analysis. Approximately half of the sample was female ($n = 12$). Child participants had a mean age of 11.41 years ($SD = 0.55$). Note that a subset of this sample was included in Paper II ($N = 30$; *Mean age* = 11.35; $SD = 0.52$; 11 girls), due to stricter inclusion criteria, whereas Papers III and IV featured the full count of thirty-seven individuals passing basic data quality control standards.

The remaining subset of 54 participants were typically developed adults, 18–33 years old. A total of forty-four (Paper II; *Mean age* = 23.69; $SD = 2.63$), forty-six (Paper I; *Mean age* = 23.83; $SD = 3.28$), and fifty-one (Paper III; *Mean age* = 23.36; $SD = 2.86$) participants from the same adult subject pool were included in the analyses performed for this thesis. Gender distributions of the adult sample amounted to 29 women and 22 men ($N = 51$). See Table 1 for an overview of participant demographics associated with each paper.

Table 1.

Participant demographics (after exclusion).

Paper	Children (<i>N</i>)	Age <i>M</i> (<i>SD</i>)	Adults (<i>N</i>)	Age <i>M</i> (<i>SD</i>)
I	0	–	46	23.83 (3.28)
II	30	11.35 (0.52)	44	23.69 (2.63)
III	37	11.41 (0.55)	51	23.36 (2.86)
IV	37	11.41 (0.55)	0	–

N: number of participants. *M*: mean age. *SD*: standard deviation.

3.1.1. Ethical considerations

All studies were performed in accordance with the ethical principles of medical research involving human subjects, as outlined by the Declaration of Helsinki (World Medical Association, 2013). The collection of neuroimaging data in children (Papers II–IV) and adults (Papers I–III) was approved by the Regional Ethical Review Board in Linköping, Sweden (child study approval reference: 2018/513-32; adult study approval reference: 2017/103-31). As detailed in information letters distributed for the two studies, anatomical scans obtained for each participant were reviewed by a licensed radiologist and passed on to a physician in the event of detected irregularities.

Adult participants provided written informed consent for their participation in the study. This document detailed their right to withdraw from the study at any point in time, without the need to specify a reason for doing so.

The inclusion of child participants required additional ethical considerations. Given that underage children are not legally authorized to give their consent for participation in research (Swedish Code of Statutes, SFS 2003:460, 18§), this required the written informed consent of a legal guardian. We furthermore required the legal guardian to accompany their child to the neuroimaging session. However, we also mandated the verbal assent of participating children in order

to avoid coerced participation. SFS 2003:460 requires that participants under the age of 15 understand the purpose of the study before giving their assent, which led to the creation of two information letters covering the same general content but individually adapted to the reading level of children and adults. This information included a research plan, overview of experimental tasks, a description of the methods, risks, and a statement on the right to withdraw from the study at any time. All rights detailed by the informed consent (i.e., full information about the purpose of the study, methods, possible risks, names and contact information for all personnel, and statement on voluntary participation) also applied to participants' legal guardians.

Functional magnetic resonance imaging (fMRI) is a non-invasive and safe tool for studies of brain activity (Kanal et al., 2013; van Osch & Webb, 2014). There is now a substantial collection of research indicating that the method is as safe for use in children as in adults. For instance, a study by Holland et al. (2014) performed a longitudinal evaluation of children who performed up to ten fMRI sessions within the scope of two years, and did not find any atypical changes in intelligence, language development, executive functions, weight, or height up to ten years after their participation (cf. Thomason, 2009).

3.2. fMRI

Functional magnetic resonance imaging (fMRI) is one of the most commonly employed neuroimaging methods for studying the neural bases of human behavior and cognition. Replacing earlier technologies such as Positron Emission (PET), which required introduction of radioactive trace chemicals into the bloodstream, fMRI is a non-invasive and safe means of examining local blood oxygenation (e.g., Poldrack, Mumford, & Nichols, 2011). The blood-oxygen-level-dependent (BOLD) contrast leverages the magnetic properties of oxygenated hemoglobin, supplied through the bloodstream as neural metabolic demands increase, which is interpreted as a proxy for neural activity. Participants are placed inside an MRI scanner, where a strong magnetic field (commonly 3

Tesla) is generated in order to localize significant increases in magnetically resonant oxygenated blood throughout the brain. Function–structure hypotheses, investigating the location of significantly activated neural clusters during specific cognitive processes (e.g., Klein, 2010), can be performed by administering a number of relevant experimental tasks for participants to perform while situated in the MRI scanner. Typically, such a research paradigm also involves the use of control tasks, used to subtract task-irrelevant activity from that obtained from experimental tasks. The ideal control task shares the highest possible degree of perceptual features and response demands with the experimental task but does not target the precisely delineated cognitive process of interest, as informed by a study’s research questions and hypotheses.

While a multitude of applications exist for the analysis of fMRI data, this thesis focuses on three main approaches: the common mass-univariate general linear model (GLM) analysis; the analysis of functional connectivity (fcMRI) between neural regions of interest (ROI); and a novel, machine learning-based method (connectome-based predictive modeling) for identifying correlations between patterns of functional brain connectivity and separately administered behavioral outcome measures. Additional details for each method can be found in chapter 4 and Papers I–IV (cf. Soares et al., 2016).

3.3. Experimental design and stimuli

3.3.1. Behavioral study design

All participants performed a cognitive-behavioral testing session prior to their participation in the neuroimaging studies covered by Papers I–IV. Behavioral data collected from the adult participant sample has not been analyzed in the featured papers and is therefore outside the scope of this thesis. Interested readers are encouraged to read Skagerlund et al. (2019) and Skagerlund, Forsblad, Tinghög, and Västfjäll (2021) for further details.

Participating children, included in Papers II–IV, performed a behavioral testing session lasting approximately two hours. The purpose of this session was to both provide measures of domain-specific and domain-general cognitive ability, as well as to familiarize participants with the forthcoming tasks administered during the neuroimaging session. A subset of collected behavioral data is presented in Papers II and IV. Relevant measures are fully described in the Supplementary Materials for the two papers.

In brief, the full session consisted of the following behavioral measures: arithmetic ability (addition, subtraction, and multiplication fluency; mental addition and subtraction calculations; and addition, subtraction, and multiplication arithmetic equation problems with a missing term); non-verbal intelligence (subsets B–D of Raven’s Standard Progressive Matrices; Raven, 1976); visuospatial mental rotation (alphabetic letters and three-dimensional cuboid perspective line drawings; cf. Rüsseler et al., 2005; Shepard & Metzler, 1971; Vandenberg & Kuse, 1978); reading ability (Malmquist, 1977); math anxiety (Scale for Early Mathematics Anxiety; Wu et al., 2012); cardinal number discrimination (identical to the Arabic digit comparison neuroimaging task); non-symbolic number discrimination (Panamath; Halberda, Mazocco, & Feigenson, 2008); verbal working memory (cf. Östergren & Träff, 2013); visuospatial working memory (self-developed); ordinal processing (numerical, alphabetical, and nonsymbolic; corresponding to the symbolic ordinal number processing neuroimaging task); and executive function (Trail Making Test and color Stroop task; van der Sluis, de Jong, & van der Leij, 2004).

3.3.2. Neuroimaging study design

The two neuroimaging studies, performed with adult and child participants respectively, were conducted at the Center for Medical Imaging and Visualization (CMIV), Linköping University. Neuroimaging data was acquired using a Siemens Magnetom Prisma MRI Scanner (3 Tesla) coupled with a twenty-channel head coil.

3 (three, ●●●). Methods

Prior to the experimental testing session, structural-anatomical scans were acquired using a T1-weighted pulse sequence. These scans were used both for review by a licensed radiologist, in the event of detected abnormalities, and for later alignment of functional data. A total of 208 slices, with a thickness of 0.9 mm³, were collected in order to generate a whole-brain structural-anatomical scan for each participant (TR = 2300 ms, TE = 2.36 ms, flip = 8°). Task-based functional scans were acquired with an ascending Echo Planar Imaging (EPI) pulse sequence, leveraging the BOLD-sensitive T2*-weighted imaging sequence. Forty-eight (48) slices were collected with a repetition time of 1340 ms (TE = 30 ms, flip = 69°) in order to obtain whole-brain coverage. The MRI hardware and scanning protocol were held constant across both studies.

Each neuroimaging session consisted of the following steps: acquisition of structural-anatomical scans, performance of the first 7-minute experimental task run, acquisition of Diffusion Tensor Imaging data (DTI), performance of the second 7-minute experimental task run, acquisition of resting-state fMRI data (cf. Skagerlund et al., 2019), and concluded with the third 7-minute experimental task run. Participants were instructed to lie still and relax during DTI and resting-state data acquisition, serving as leisurely breaks of approximately 6 and 10 minutes, respectively.

Four tasks were common to both studies, targeting the TCM: the Arabic digit comparison task, the verbal number comparison task, the nonsymbolic magnitude comparison task (adapted from Halberda et al., 2008), and the letter case discrimination control task. For the adult study, two additional tasks outside the scope of this thesis were administered (cf. Skagerlund et al., 2021). The child study featured two additional tasks, featured in Paper IV: the symbolic ordinal number processing task and its associated symbolic congruity comparison control task. See Figure 1 for an overview of administered tasks.

All tasks followed the same basic visual presentation and response characteristics. A block of 14 trials was preceded by a brief written instruction (e.g., “larger

number/letter?”, “correct order?”, or “identical symbols?”), lasting for two seconds. Each individual trial spanned 4000 ms, which included a 500 ms presentation of a fixation cue (“+”), 2000 ms stimulus presentation (e.g., “3 6”), and concluded with a 1500 ms response window (indicated by a visually presented question mark). Participants were instructed to respond during the response window, using one of two response pad buttons (see Figure 1). Reaction time and accuracy data were not collected before the visual presentation of the response window.

TCM-related tasks (i.e., Arabic, verbal, and nonsymbolic numerical magnitude comparisons) consistently requested participants to select the numerically larger option out of two visually presented alternatives. The associated letter case discrimination control task applied this principle to the alphabetical domain, requesting participants to select the uppercase letter. This affords identical response criteria across tasks, as Swedish colloquially refers to uppercase letters as “large letters” as opposed to the lowercase “small letters”. Thus, both the experimental numerical tasks and the control task had identical requirements of selecting the “larger” option. The symbolic ordinal number processing task (adapted from Lyons & Beilock, 2013) featured Arabic digit triplets (e.g., “1 2 3”), requesting participants to press the right-hand response button if the sequence was correctly ascending or descending, or to press the left-hand button if the sequence was in a mixed, non-sequential order (e.g., “1 5 3”) . The associated symbolic congruity comparison control task used a similar triplet format, requesting participants to indicate whether the three symbols were congruent (e.g., “Y Y Y”) via right-hand button response, or to press the left-hand button if the trial was incongruent (e.g., “A 2 A”).

Figure 1. Experimental design of the neuroimaging studies. Top rows illustrate far-distance trials (first half of each run), bottom rows illustrate near-distance trials (second half of each run).

4. Summary of papers

The following chapter will serve as a summary of the theoretical background, aims, methods, results, and key findings associated with Papers I–IV.

4.1. Paper I

4.1.1. Background and aims

The triple code model of numerical cognition (TCM), as first developed by Dehaene (1992), holds that both partially overlapping and separable, functionally distinct neural correlates govern the processing of numerical stimuli in three primary representational codes: the visual Arabic number form (e.g., “1”), the auditory verbal word frame (e.g., “two”), and analog nonsymbolic representations of numerical magnitude (e.g., ●●●). The division of numerical cognition into three discrete representational codes carries implications for the acquisition and deployment of numerical concepts. Whereas approximate representation of nonsymbolic numerical magnitude is argued to be a biologically predisposed capacity, as evidenced by its occurrence in preverbal infants and non-human animals alike (e.g., Starkey & Cooper, 1980; Brannon, Jordan, & Jones, 2010), symbolic number processing is a culturally transmitted and effortfully learned ability (e.g., Núñez, 2017). The TCM suggests that the biologically predisposed neurocognitive basis for approximate number representation is eventually leveraged to give meaning to number symbols, allowing the emergence of more complex numerical operations—such as arithmetic—over developmental time. This view has developed from empirical evidence, demonstrating that similar performance in number discrimination tasks is achieved regardless of whether Arabic digits or collections of dots are used as stimuli. Given that performance, in terms of reaction time and accuracy, is altered primarily by the ratio between the compared number stimuli rather than the numerical format, it is argued that symbolic numbers (such as Arabic digits) gain their semantic

content from a mapping onto the quantity representations in the ANS (Moyer & Landauer, 1969; Dehaene, 2003).

Early proposals of the model (e.g., Dehaene, 1992; Dehaene & Cohen, 1995) primarily based their suggested neural correlates of number processing on single-case deficit studies, psycholinguistic research, and six postulates outlining basic neuroanatomical facts—covering issues such as lateralization of function, functional neural pathways, and the role of semantic versus asemantic processing of numerical stimuli. While often cited and referenced in both cognitive-behavioral and neuroimaging-based research, no study prior to the publication of Paper I had systematically examined the neural correlates of each representational code within the scope of one neuroimaging study, nor the extent to which the conjunctive neural activity across all three codes could explain the underlying overlap in cognitive processes required for basic number discrimination. To this end, the aim of Paper I was to empirically investigate the functional neural correlates hypothesized by the TCM, and—by extension—the validity of the model itself.

We predicted that the neural correlates associated with each code would generally correspond to predictions by Dehaene and Cohen (1995), adjusted for more recent findings of a frontoparietal functional brain network implicated in number processing tasks (e.g., Fias et al., 2013; Sokolowski et al., 2016; Jolles et al., 2016). For the Arabic code, we hypothesized that the so-called visual number form area—approximately located within the right inferior temporal gyrus (ITG; e.g., Shum et al., 2013)—would demonstrate increased activity as compared to the verbal and nonsymbolic codes. Such a result implies that the region undergoes ontogenetic domain-specialization in service of processing visual Arabic digit stimuli, consistent with similar findings for visually presented letters and words (e.g., Polk et al., 2002). The verbal code, given its increased reliance on linguistic capabilities, was hypothesized to demonstrate an increased dependence on the left-lateralized perisylvian language network, featuring the following central neural correlates: the supramarginal (SMG), inferior frontal (IFG), middle temporal (MTG), and superior temporal (STG) gyri (e.g., Schmithorst &

Douglas Brown, 2004; Dehaene et al., 2003). Although the left angular gyrus (AG) should be considered a node of the perisylvian language network, previous research in number processing suggests that the region plays a broader role in the representation of numerical information across multiple formats beyond the verbal code (e.g., Price & Ansari, 2011). Common to all tasks, but particularly the nonsymbolic code, we expected to find consistent activation in the bilateral horizontal segment of the intraparietal sulcus (IPS), given its purported role as the primary neural correlate of numerosity judgments and the region where symbolic numerical stimuli are mapped against the approximate number system (e.g., Nieder & Dehaene, 2009). Taking an exploratory approach, we reasoned that the predictions of the TCM would act as a form of “ground truth”, whereas any deviations would be indicative of a need for revising the model.

4.1.2. Methods

Forty-six right-handed, healthy adult university students (*Mean age* = 23.83, *SD* = 3.28; 20 males and 26 females) participated in an fMRI-based study. Three experimental tasks were administered, corresponding to the three representational codes outlined by the TCM. Common to all tasks, participants were requested to select the numerically larger visual stimulus out of two concurrently presented alternatives. A control task was also administered (see section 3.3.2), requesting participants to select the alphabetical letter presented in uppercase notation (e.g., “a” versus “F”). An alternating blocked design with a fixed task order was used, spanning three Echo Planar Imaging (EPI) runs (see Figure 1). Each of these runs were divided into two iterations, manipulating the numerical distance of presented stimuli, such that the first iteration consisted exclusively of far-distance number comparisons (e.g., “3 vs 7”; “three” versus “seven”; or 12 versus 24 dots) and the second iteration consisted of near-distance comparison tasks (e.g., “4” versus “5”; “four” versus “five”; or 10 versus 13 dots). Each task block featured 14 trials, resulting in a total of 84 trials per task (i.e., 14 trials per block $\times$ 2 block iterations per EPI run $\times$ 3 EPI runs) over the course of the experiment. Each individual trial was presented for a total of 4000 ms: including an

initial fixation cue (500 ms), stimulus presentation (2000 ms), and response window (1500 ms). Two additional tasks beyond the scope of this thesis—featuring risk and benefit judgments—were also administered (cf. Skagerlund et al., 2021).

Eight statistical contrast analyses were performed on the task-based functional neuroimaging data. For each of the experimental tasks, we subtracted activity related to the control task as to exclude task-irrelevant neural activation patterns. This resulted in three contrast analyses, for the Arabic (i.e., [Arabic > Control]), verbal (i.e., [Verbal > Control]), and nonsymbolic (i.e., [Nonsymbolic > Control]) codes. In order to investigate the neural correlates associated with the numerical distance effect, activity elicited by far-distance trials was subtracted from corresponding near-distance trials. This resulted in three parametric contrast analyses investigating activity uniquely elicited by near-distance Arabic digit comparison (i.e., [Arabic_{Near} > Arabic_{Far}]), verbal number comparison (i.e., [Verbal_{Near} > Verbal_{Far}]), and nonsymbolic magnitude comparison (i.e., [Nonsymbolic_{Near} > Nonsymbolic_{Far}]) trials. Note that Paper I refers to the near and far-distance contrasts as “close” and “distant”, respectively, whereas this thesis will henceforth use the terms “near” and “far” for consistency with Papers II–IV. Finally, two conjunction analyses were performed with the purpose of identifying consistently overlapping activation of neural correlates across all three number processing tasks. The first conjunction analysis targeted experimental task-based activity subtracted by the control task (i.e., [Arabic > Control] $\cap$ [Verbal > Control] $\cap$ [Nonsymbolic > Control]), whereas the second pertained to overlapping activation across the near-distance trials of each experimental task (i.e., [Arabic_{Near} > Arabic_{Far}] $\cap$ [Verbal_{Near} > Verbal_{Far}] $\cap$ [Nonsymbolic_{Near} > Nonsymbolic_{Far}]). Beyond whole-brain analyses, theoretically informed region of interest (ROI) analyses were performed in the bilateral IPS, right ITG, left IFG, STG, SMG, and MTG.

4.1.3. Results and Discussion

Emerging as the single largest finding of the study, the control task-subtracted conjunction analysis revealed a pattern of both bilateral neocortical and subcortical activity common to all three codes of the TCM. Notably, this conjunctive activity did not include the intraparietal sulcus, argued to be the key functional neural correlate of numerical magnitude processing (e.g., Ansari, 2008). This absence is driven by the lack of IPS activation during the nonsymbolic task, hypothesized to interfere with a similar spatial magnitude discrimination taking place in the control task (see Paper II for an extension of this argument). Diverging from predictions of the TCM, but in agreement with more recent empirical research detailing the importance of contralateral functional connectivity patterns (e.g., Moeller, Willmes, & Klein, 2015; Price et al., 2018), this substantial spatial coverage indicates the necessity of adopting a functionally distributed neural network perspective in the domain of numerical cognition. While exceeding the predictions of the TCM, which are restrictive in nature due to more modular conceptions of cognitive neuroscience at the time of its inception, observed overlapping neural activity was found to align better with proposed updates based on recent meta-analyses (Arsalidou & Taylor, 2011). In agreement with these proposals, participants were observed to recruit the dorsolateral and ventromedial prefrontal cortex, angular gyrus, left insula, and anterior cingulate cortex; suggesting interactions between the frontoparietal, default mode, and salience networks (cf. Fias et al., 2013).

The parametric conjunction analysis resulted in a single suprathreshold voxel within the left intraparietal sulcus. This outcome is in alignment with prior findings of the region's involvement in effortful number processing, such as arithmetic (e.g., Simon et al., 2002) and near-distance number discrimination (e.g., Ansari & Dhital, 2006), but should be interpreted cautiously given the limited spatial extent. While discussed in greater length in section 5, as well as in Papers II–III, it should be noted that such limited overlap could also be the result of a disentanglement of symbolic and nonsymbolic number processing in adulthood.

More recent empirical evidence gathered for this thesis strongly favors the idea that symbolic numbers are potentially mapped to the ANS in children, but that these mechanisms become separated over the course of neurocognitive maturation, allowing number symbols to be understood in relation to other symbol-based referents (cf. Reynvoet & Sasanguie, 2016).

The main effects of each numerical representational code were examined using control task-subtracted and parametric (i.e., corresponding to the numerical distance effect) statistical contrasts. For the Arabic digit comparison task, activity was elicited in a previously proposed candidate region for the visual number form area (cf. Yeo, Wilkey, & Price, 2017) and was furthermore observed to elicit higher activation magnitude (i.e., beta values) compared to the verbal and nonsymbolic tasks. This outcome aligns with the TCM and its prediction of a code-specific visual processing region for Arabic digits (e.g., Dehaene & Cohen, 1995). However, activity was also observed to span large clusters of the visual cortex, MTG and insula (respectively associated with semantic memory and salience), IFG (associated with working memory processes), basal ganglia (associated with learning and memory; Arsalidou & Taylor, 2011), and dorsolateral prefrontal cortex (associated with cognitive control and working memory; cf. Fias et al., 2013). This outcome indicates substantial complexity beyond the predictions of the TCM. For the verbal number comparison task, activity was observed to follow a similarly distributed pattern as described for Arabic digit processing. In line with predictions of the TCM, the task recruited several perisylvian language regions (e.g., IFG and MTG), but notably also elicited unique activity in the left hippocampus corresponding to Dehaene and Cohen's (1997) prediction of a rote verbal number retrieval circuit. The nonsymbolic task elicited decisively less spatially extended activity, localized primarily in the visual cortex, anterior and middle cingulate cortices, basal ganglia, and dorsolateral as well as ventromedial prefrontal cortex. This suggests mechanistic differences in the processing of symbolic and nonsymbolic number representations, and the extensive visual cortex recruitment—in particular—could be indicative of a stronger reliance on

low-level visuospatial processing mechanisms for nonsymbolic magnitude discrimination (cf. Fornaciai et al., 2017; Roggeman et al., 2011; Cavdaroglu, Katz, & Knops, 2015). Finally, the parametric contrasts indicated a consistent pattern of activation in the left IPS across tasks, advocating the region as a primary neural correlate of the numerical distance effect and invoked in line with increased numerical complexity (such as for arithmetic operations; e.g., Ansari & Dhital, 2006; Simon et al., 2002; Sokolowski & Ansari, 2016).

In summary, the results of Paper I provide an updated and comprehensive mapping of the neural correlates associated with the TCM. The main takeaway of Paper I lies in empirically validating that numerical cognition, across the three representational formats, recruits a multitude of domain-general neural correlates associated with—among others—working memory, cognitive control, and visuospatial attention (cf. Iuculano, Padmanabhan, & Menon, 2018). The predictions of the TCM therefore provide a relevant account of domain-specific number processing mechanisms, accounting for a degree of domain-generality (e.g., language), but require substantial updates in line with state-of-the-art neurocognitive research.

4.2. Paper II

4.2.1. Background and aims

Developmental maturation effects govern the emergence of increasingly more sophisticated numerical discrimination abilities. Although the capacity for non-symbolic approximate number discrimination is present from birth, it operates with low acuity in early infancy and is initially limited to ratios of 1:2, or the capacity to reliably discriminate—for instance—numerical dot arrays differing by half or double the numerosity. At approximately 10 months of age, this capacity matures to the extent that a ratio of 2:3 (e.g., 12 versus 18 dots) can be reliably discriminated (Xu & Spelke, 2000), eventually culminating in the discrimina-

bility of a 9:10 ratio (e.g., 18 versus 20 dots) in adulthood (Halberda & Feigenson, 2008). Such ratio effects also emerge for the symbolic number codes at approximately five years of age, indicating a bootstrapping of newly acquired symbolic number representations onto the approximate number system (ANS; cf. Nieder & Dehaene, 2009; Odic & Starr, 2018). Consistent distance and size effects across symbolic and nonsymbolic number discrimination tasks, as evidenced by psychophysical measures of response time and task accuracy, further support a common representational basis for number processing (cf. Moyer & Landauer, 1967). This common representational basis may be found in the approximate number system, as argued by the TCM (e.g., Dehaene, 1992; Dehaene & Cohen, 1995).

In line with the ANS bootstrapping hypothesis, the TCM argues that symbolic number referents gain their numerical meaning by being mapped to the ANS. This position is supported by at least four lines of evidence. First, ANS acuity in infancy has been observed as a strong predictor of later mathematics achievement (Starr et al., 2013). Second, practice of approximate arithmetic—using nonsymbolic numerical dot arrays for addition tasks—improves both preschoolers’ and college students’ symbolic arithmetic ability (Park et al., 2016). Third, ANS acuity is not influenced by practicing symbolic arithmetic (Lindskog et al., 2016), suggesting the primacy of the ANS for the development of numerical cognition. Fourth, the TCM holds that the primary neural correlate of the ANS, the intraparietal sulcus (IPS), is consistently engaged in number discrimination tasks across representational codes (e.g., Dehaene et al., 2003). However, prior research has provided inconsistent evidence for the purported similarity in number discrimination performance across codes; their degree of overlapping neural activity patterns; and different representational codes’ consistency of impact on future mathematics achievement (cf. Reynvoet & Sasanguie, 2016). Such conflicting results motivated the investigation of neural correlates associated with the TCM in both adults and children, as well as potential developmental differences that may shed additional light on the acquisition and deployment of symbolic number processing abilities.

4 (four, ●●●). Summary of papers

Similar to the adult population, the neural correlates of the entire TCM had not been investigated—in the context of basic number discrimination tasks—in children prior to Paper II. The aim of this study was therefore to provide an overview of the neural correlates associated with typically developing children’s number processing across all three representational codes, as well as to identify key developmental differences between children and adults. Furthermore, the outcomes of this study act as a means of validating previous meta-analytic research (e.g., Arsalidou & Taylor, 2011; Arsalidou et al., 2018), providing a direct and relatively unbiased (in terms of employing the same hardware, using a common data processing pipeline, and comparing the same set of experimental tasks) empirical comparison between children and adults. The aforementioned meta-analyses served as the basis for our hypotheses in Paper II, although it should be noted that the study primarily employed an exploratory approach. Given that the sample of adult participants was a subset of those reported in Paper I, our hypotheses primarily targeted the novel child participant sample and their unique recruitment of neural correlates, as well as those potentially shared with adults.

We predicted that participants of both age-groups would primarily exhibit shared activity in the right inferior frontal gyrus (IFG), cingulate gyrus, and bilateral intraparietal sulcus (IPS), insula, and middle frontal gyrus (MFG) across the three tasks (cf. Arsalidou & Taylor, 2011; Arsalidou et al., 2018). Similarly, for each of the experimental tasks but particularly so for the nonsymbolic code, we predicted that both age-groups would exhibit consistent activation of the bilateral IPS in accordance with the TCM (e.g., Dehaene et al., 2003). In children’s overall symbolic number processing, given the scarcity of previous research on the verbal code in children, we expected increased reliance on the right IFG as well as pre- and postcentral gyri (cf. Libertus et al., 2009). Such an outcome aligns with previous accounts of a frontal-to-parietal migration of symbolic number processing as a consequence of ontogenetic maturation (e.g., Ansari et al., 2005; Libertus et al., 2009). Moreover, we reasoned that symbolic number

processing in general would elicit an increased reliance on symbol-to-magnitude mapping processes governed by the left SMG and right superior parietal lobe and IPS (e.g., Park et al., 2014; Skagerlund et al., 2019). As was the case for Paper I, these hypotheses served as guiding “ground truth” predictions anchored in the TCM, while additional outcomes constituted avenues for further exploration.

4.2.2. Methods

Thirty children ($N = 30$; Mean age = 11.35; $SD = 0.52$) and forty-four adult university students ($N = 44$; Mean age = 23.69; $SD = 2.63$) participated in the study. All participants were right-handed and had no self-reported or prior clinically documented general health issues, neurological illnesses, or mathematical difficulties.

We administered the same three experimental tasks described for Paper I, targeting each code of the TCM (i.e., Arabic, verbal, and nonsymbolic number comparison), as well as the same control task (see also section 3.3.2). The child study included two additional tasks (replacing the risk and benefit judgments detailed in Skagerlund et al., 2021) beyond the scope of Paper II, which were fully analyzed in Paper IV (cf. section 3.3.2). In direct accordance with the experimental design of Paper I, participants were instructed to select the numerically larger stimulus out of two concurrently visually presented options across all three experimental tasks. Similarly, the letter case discrimination control task was identical to that described in Paper I. Trial counts, number of task blocks, and trial presentation times were identical across child and adult data collection sessions, with the acquisition of child data occurring approximately 1.5 years after the completion of adult data collection.

Five planned statistical contrast analyses were performed on the task-based functional neuroimaging data. Two-sample T-test analyses were performed for each of the experimental tasks, investigating between-group (i.e., children versus adults) differences for each representational code (i.e., [Task > Control]).

For these three statistical contrasts, near and far-distance trials of each task were collapsed into a singular overall task activity measure. Parametric comparisons between near and far-distance trials—in line with the numerical distance effect—were performed and included as supplementary results for completeness. Two additional statistical contrasts were performed for the conjunction analyses. The first featured a control task-subtracted conjunction of task-related activity across both age-groups (i.e., [Arabic > Control] $\cap$ [Verbal > Control] $\cap$ [Nonsymbolic > Control]), indicative of overlapping neural correlates for the three experimental tasks in both children and adults. The second, parametric conjunction analysis (i.e., [Arabic_{Near} > Arabic_{Far}] $\cap$ [Verbal_{Near} > Verbal_{Far}] $\cap$ [Nonsymbolic_{Near} > Nonsymbolic_{Far}]) was performed as a means of determining overlapping neural correlates of the numerical distance effect—across all three codes—in both children and adults. Unexpected results (further detailed in section 4.2.3) prompted the administration of two post-hoc exploratory conjunction contrasts, targeting an inverse task–control subtraction (i.e., [Control > Tasks]) and a conjunction analysis of the symbolic codes (i.e., [Arabic > Control] $\cap$ [Verbal > Control]) across both participant groups.

4.2.3. Results and Discussion

Two 2 (group: child, adult) $\times$ 4 (task: Arabic, verbal, nonsymbolic, control) Bonferroni-corrected, repeated-measures analyses of variance (ANOVA) were performed to investigate the distribution of response times and accuracies across tasks administered during neuroimaging data collection. A main effect of both group and task was identified for response times, indicating that adults performed all tasks significantly faster than children. Response accuracy demonstrated a main effect of task, where all participants were observed to correctly answer more trials of the Arabic, verbal, and control tasks compared to the nonsymbolic number comparison task.

4 (four, ●●●). Summary of papers

Two conjunction analyses were performed, targeting the overlap in neural activity elicited by experimental tasks as subtracted by the control task (control-subtracted conjunction), as well as the overlap elicited by parametric comparison of the numerical distance effect across tasks (parametric conjunction).

The control-subtracted conjunction analysis resulted in a single cluster of joint activity within the right lingual gyrus, corresponding to a key node of a previously identified bilateral occipito-parietal network implicated in visual number comparisons (Leibovich & Ansari, 2017). This unexpectedly low degree of overlapping neural activation in children and adults affords two potential explanations. First, Walsh's (2003) A Theory of Magnitude argues for a common generalized magnitude processing system—anchored in the intraparietal sulcus (Buetti & Walsh, 2009)—for the domains of space, time, and number. It could be argued that the control task is processed as a spatial magnitude comparison, given that surface area is often sufficient to distinguish between uppercase and lowercase letters (e.g., “a” versus “A”). In this vein, the lack of a minimally expected joint IPS activation across tasks and participant groups could be due to the performance of a spatial magnitude comparison, inherent to the control task, subtracting such activity from the experimental tasks. Support for this position is found in the post hoc “inverse” conjunction analysis (i.e., $[\text{Control} > \text{Arabic}] \cap [\text{Control} > \text{Verbal}] \cap [\text{Control} > \text{Nonsymbolic}]$), which resulted in suprathreshold bilateral intraparietal sulcus activity. A second potential source of absent control-subtracted conjunction across tasks and participant groups was found in the post hoc symbolic number task conjunction analysis (i.e., $[\text{Arabic} > \text{Control}] \cap [\text{Verbal} > \text{Control}]$), indicating that activity was significantly more consistent across the symbolic than nonsymbolic codes. Adults and children were found to jointly recruit the bilateral postcentral and supramarginal gyri; the right lingual gyrus, as well as the left insula, which aligns with previous meta-analytic results in adults (Arsalidou & Taylor, 2011). This outcome could suggest that developmental differences in the processing of nonsymbolic numerical magnitude are the main driver of scarce control-subtracted conjunction overlap, but also lends credence to the hypothesis that a spatial magnitude comparison—inherent to the

control task—subtracts similarly elicited activity from the experimental tasks. That is, nonsymbolic magnitude comparison may be particularly vulnerable to unintended task-related activity subtraction from the control task, given that this representational code is also closely intertwined with visuospatial extent cues such as surface area (cf. DeWind et al., 2015).

The parametric conjunction analysis indicated substantially more overlap in neural activity across tasks and participant groups. Although parametric analyses have the benefit of only featuring task-related activity, such an approach comes with the caveat of potentially reducing activity common to both near and far-distance trials. Remaining activity in near-distance trials across all three codes of the TCM indicated that the child participant group shared several neural correlates previously described for adult-level number processing (Arsalidou & Taylor, 2011). Consistent patterns of activity were observed throughout the dorsal (e.g., superior and inferior parietal lobe, posterior-medial frontal cortex, and supplementary motor area) and ventral (e.g., inferior frontal and angular gyri) frontoparietal networks. Novel overlap between children and adults was also identified in the bilateral cerebellum, previously only identified in meta-analyses of adult-level number processing (Arsalidou & Taylor, 2011).

Together, the parametric conjunction and post hoc symbolic code-conjunction analyses indicate significant similarities in the recruitment of neural correlates for number discrimination tasks in 11-year-old children and young adults. This outcome suggests that numerical magnitude discrimination abilities reach an adult-level developmental maturation stage at the observed ontogenetic timepoint, in line with research indicating the diminishing importance of such skills for mathematical achievement from approximately 10–12 years of age (Lyons et al., 2014). Further support for this position is found in the numerical representation code-specific analyses of developmental differences, investigating age-dependent differences in the activation of neural correlates associated with the Arabic, verbal, and nonsymbolic codes. Neither of these analyses indicated the existence of neural correlates uniquely recruited by children, whereas adults

predominantly elicited activity in neural regions (e.g., anterior and middle cingulate cortices) associated with domain-general cognitive control mechanisms (cf. Shenhav et al., 2016). Such results could be taken to suggest that adults and middle-school-aged children fundamentally process numerical information in a similar manner, but that adults manipulate numerosity more efficiently as a result of developmentally mature executive functioning abilities. This view is supported by adults' significantly lower response times across all tasks, despite comparable accuracy rates in both participant groups.

The verbal code constituted a notable exception to adults' otherwise consistent, unique recruitment of correlates associated with cognitive control. For this task, adult participants demonstrated activity in perisylvian language areas (particularly middle temporal and inferior frontal gyri, as well as the insula), in line with predictions of the TCM (e.g., Dehaene & Cohen, 1997). This pattern may reflect the maturation of a ventral frontal-temporal-parietal network (cf. Brauer et al., 2013) that has previously been argued to support both numerical and linguistic semantic classification abilities (Willmes et al., 2014). Consequentially, this uniquely adult recruitment of perisylvian language network nodes calls for a child-specific conception of the triple code model's verbal code and further research into the neurocognitive mechanisms required for verbal number processing in children. A hypothesis for future research regarding this issue is that adults' increased recruitment of language regions also constitutes a correlate of mature cognitive flexibility, suggesting that increased exposure to written verbal representations of number establishes discrete lexico-semantic numerical categories that can be retrieved rather than mapped against the ANS (cf. Verguts et al., 2005; Lyons & Beilock, 2018).

4.3. Paper III

4.3.1. Background and aims

The results obtained in Paper II suggest that approximately 11-year-old children's numerical discrimination abilities operate with near-adult level maturity, as evidenced by substantial overlap in the recruitment of neural correlates. However, inferring that no—or minor—neurodevelopmental maturation effects associated with the refinement of number discrimination abilities occur between (approximately) 11–24 years of age is untenable on at least four grounds. First, the fact that adults were observed to perform all three number discrimination tasks significantly faster than children, while maintaining near-perfect accuracy, is indicative of developmentally mediated performance gains. If so, such gains are unlikely to occur without some measurable impact on neurocognitive function. Second, a large body of prior empirical evidence suggests that numerical cognition is subject to developmental maturation effects from early childhood to late adulthood (e.g., Svenson & Sjöberg, 1983; Uittenhove et al., 2015; Cappelletti et al., 2014; Norris et al., 2015; Halberda et al., 2012; Salthouse & Coon, 1994). For instance—and in agreement with the findings of Paper II—adding an additional dot to a nonsymbolic subitization task has been observed to increase response times threefold in children compared to adults (Svenson & Sjöberg, 1983). According to the developmental calculation model (Kaufmann, Wood, Rubinsten, & Henik, 2011), different types of numerical representations become more integrated as a result of age, schooling, and the further development of domain-general cognitive abilities (e.g., visuospatial attention, language, and working memory). Such integration of symbolic and nonsymbolic number processing should also be observable in measures of neural correlates. Third, neurocognitive research indicates substantial differences in the coactivation and communication within functional neural number processing circuits for children and adults (cf. Iuculano, Padmanabhan, & Menon, 2018). For instance, in the case of arithmetic fact retrieval, children demonstrate an in-

creased reliance on early memory consolidation processes in the medial temporal lobe (MTL) memory system, as opposed to adult-level recruitment of retrieval-based neocortical memory systems (Cho et al., 2012). Fourth, recent research increasingly questions the extent to which ANS-based measures explain symbolic number processing abilities, particularly so from adolescence and onward (e.g., Lyons et al., 2014). Such outcomes suggest that symbolic numbers may increasingly be processed independently of the ANS, which should be reflected by associated developmental differences in functional connectivity between neural correlates of approximate quantity and symbol-based semantic processing.

Taken together, neurocognitive differences appear likely to be observable given the lack of a speed–accuracy tradeoff during adult participants’ number discrimination, prior evidence of behavioral differences over the course of ontogeny, manifest differences in the recruitment of functional neural circuits in numerical processing tasks, and the increasingly likely dissociation of symbolic and nonsymbolic number processing mechanisms across development. These four considerations are by no means exhaustive, but rather serve to illustrate that neurocognitive differences in child and adult number processing are to be expected. A possible interpretation for this apparent lack of neural activation differences between middle-school-aged children and adults (see Paper II), in the face of conflicting evidence, is that the 11-year-old brain may have reached a relatively mature functional-organizational state in terms of recruiting particular neural substrates for number discrimination tasks. Thus, it may rather be the case that differences could be observed on the level of functional network connectivity, between an overlapping set of neural regions commonly recruited both by “numerically mature” children and by young adults. To this end, Paper III posed two main research questions: how do the interactions between functional circuits engaged by children and adults during number discrimination differ, and are these differences modulated by different numerical representational codes as described by the TCM?

verbal, and nonsymbolic number comparison; see section 3.3.2). Near and far-distance trials were collapsed into single, code-specific conditions.

The ROI-based functional connectivity analysis was performed with the CONN toolbox for SPM12 (Whitfield-Gabrieli & Nieto-Castanon, 2012). Twenty-two regions of interest, as described above (see Figure 2), were selected from the Shen 268 node whole-brain parcellation atlas (Shen et al., 2013) and verified through comparison with commonly reported MNI coordinates and probabilistic cytoarchitectonic maps (Eickhoff et al., 2005). A parametric multivariate statistics approach was selected for the second-level analysis, as the method allows for inferences to be made for each individual region and its associated connectivity patterns.

4.3.3. Results and Discussion

Substantial differences were identified in the functional connectivity elicited between the included regions of interest, both across participant age-groups and tasks. This outcome suggests that number discrimination tasks, while leveraging a similar set of neural correlates in middle-school-aged children and young adults (see Paper II), employ qualitatively different functional neural circuits over the course of development. Notably, adults demonstrated sparse and consistent patterns of connectivity across all three codes, indicating ontogenetic domain-specialization of number processing and the integration of different numerical representational formats, in line with the developmental calculation model (Kaufmann et al., 2011).

Adult-level functional connectivity patterns suggest recruitment of the semantic control network, argued to be crucial for accessing conceptual knowledge of numerical values and their relative magnitude (cf. Sommerauer et al., 2020), as well as the default mode and frontoparietal networks (e.g., Davey et al., 2016). This is primarily evidenced by the connectivity between the right IPS, left MTG, SMG, and hippocampus, indicating an interaction between magnitude pro-

cessing (IPS) and the retrieval of semantic numerical facts (MTG, SMG, hippocampus). This interpretation is further supported by increased functional connectivity between the left IPS and hippocampus, indicative of symbolic number processing (IPS) and access to memory (hippocampus). These results suggest that adult-level symbolic number processing is dependent on semantic memory cues associated with numerical facts, leading symbolic numbers to potentially be understood in reference to other symbolic numbers, as opposed to being mapped against the ANS (cf. Reynvoet & Sasanguie, 2016). For the nonsymbolic code, developmental increases in functional connectivity were sparser and indicative of incremental refinements. Notably, adults demonstrated stronger direct connectivity between the bilateral fusiform gyrus and IPS, indicating efficient mapping of visual numerical input onto the ANS (cf. Iuculano et al., 2018). This is in line with an observed increase in functional connectivity between the left IPS and precentral gyrus, which may be taken to suggest that developmental maturation leads nonsymbolic number to be processed in a more visuospatial fashion (cf. Tomasino & Gremese, 2016) as ANS acuity increases and discrimination becomes easier to perform.

In children, unique increases in functional connectivity targeted multiple functional networks, suggesting distributed and domain-general connectivity patterns. Primarily, child-level functional connectivity indicated inhibitory connectivity in the salience and default mode networks as a consequence of increased reliance on the task-positive frontoparietal network; in line with the fact that children performed the tasks slower than adults (see Paper II). Two key patterns of functional connectivity further support the view that children rely on immature and effort-induced functional circuitry for number discrimination. First, increased connectivity between the bilateral hippocampus was present across all tasks, indicating greater demands on mapping numerical facts (right hippocampus) to stimuli held in working memory (left hippocampus; cf. Cho et al., 2012; Axmacher et al., 2007). Together with the right supramarginal gyrus connectivity—indicative of ventral attention network recruitment (Corbetta & Shul-

man, 2002)–observed across tasks, it appears likely that children are more sensitized to numerical stimuli due to an increased need for visuospatial mental number line mapping.

Overall, the results of Paper III indicate that adults understand numerical symbols in relation to other symbols, rather than having to map them against the approximate number system (cf. Reynvoet & Sasanguie, 2016). Children’s frontoparietal network dominance suggests that they require the mapping of both symbolic and nonsymbolic referents to the ANS. Developmental maturation could therefore serve the purpose of disentangling the functional circuits supporting symbolic (memory-based) and nonsymbolic (visuospatial) number processing through the ANS, while establishing functional circuitry for visuospatial, semantic retrieval, and working memory processes that provide the foundation for integrated and format-independent number processing mechanisms (cf. Kaufmann et al., 2011).

4.4. Paper IV

4.4.1. Background and aims

Research in the field of numerical cognition has predominantly focused on quantity discrimination and its impact on arithmetic aptitude. This has led to the formation of theoretical frameworks focused on the roles of approximate number system acuity and cardinal number discrimination ability, and their respective contributions to typical and deficient number processing. Developmental dyscalculia, a deficit specific to the domain of number processing (and thus not detrimental to other cognitive abilities such as attention, reading, or general intelligence), has consequently been construed as a deficit solely grounded in quantity processing (e.g., Wilson & Dehaene, 2007; Butterworth et al., 2011). This view has been challenged by the dual systems model (Rubinsten & Sury, 2011), which argues for two domain-specific core systems of number processing

that independently target numerical quantity and numerical ordinality (i.e., sequential positional value judgment) processing. That is, whereas the first system provides the foundation for determining whether five apples are more than four apples or whether “3” is a larger cardinal number than “2”, the ordinal system allows one to determine that 20° Celsius is more (i.e., warmer) than 15° Celsius but less (i.e., colder) than 30° Celsius, due to its positional value in a continuous temperature scale. These two systems are hypothesized to recruit distinct cognitive resources, primarily interfacing through language (e.g., symbolic representations, verbal count-lists, and cultural writing direction). The existence of two such separate number processing systems is strengthened by research indicating that the ordinality aspect of number can be separately impaired or spared in the case of developmental dyscalculia (Rubinsten & Sury, 2011). While such results provide compelling evidence for the existence of separable systems, the nature and potential dissimilarity of their associated neurocognitive mechanisms remains unclear.

The separability of numerical cardinality and ordinality processing mechanisms is further motivated by two main lines of evidence. First, cardinal number discrimination is characterized by a robust numerical distance effect that exhibits faster responses to numerical stimuli placed far apart (e.g., 2 versus 9) than those in close proximity (e.g., 3 versus 4; cf. Moyer & Landauer, 1967). This effect suggests the use of an item–item comparison mechanism (Vos et al., 2017), where closely related items—such as proximal numbers on the mental number line—become more difficult to distinguish than distinctly separate items. In contrast, numerical order processing exhibits a reversed distance effect (e.g., Lewandowsky & Murdock, 1989; Caplan, 2015) that entails faster responses to near-distance number triplets (e.g., whether 1-2-3 is correctly ascending) than far-distance equivalents (e.g., whether 1-3-5 is correctly ascending). This reversed distance effect is hypothesized to depend on an associative chaining mechanism, indicating that numerical order judgments are facilitated by retrieval of inter-item associations (i.e., 2 comes after 1 but before 3) stored in the long-term memory count-list (e.g., Sasanguie et al., 2017; Vos et al., 2017). The

4 (four, ●●●). Summary of papers

second line of evidence in support of separable cardinality and ordinality mechanisms concerns their differential contributions to arithmetic ability over developmental time. Although the association between cardinal number discrimination ability and arithmetic has been well-established (e.g., Booth & Siegler, 2008), numerical ordering ability has been observed to surpass cardinal magnitude discrimination as the strongest predictor of children’s arithmetic ability around the age of 10–12 years (Lyons et al., 2014). That is, while cardinal magnitude discrimination remains explanatory for mathematical competence, its impact is substantially diminished by the increased importance of being able to track and process sequential numerical relationships.

Using two separate, symbol-based (i.e., Arabic digits) numerical cardinal quantity discrimination (henceforth “cardinal”) and numerical order processing (henceforth “ordinal”) tasks, the purpose of Paper IV was to examine the separability of these mechanisms at two levels of analysis. Analyses at the level of neural activity were performed to map the neural correlates both uniquely and commonly recruited by the two tasks, as a means of determining the extent to which the two putative systems differ. A second set of analyses leveraged a brain–behavior correlation approach, investigating whether whole-brain functional connectivity patterns could predict the outcomes of separately administered domain-specific (e.g., cardinal and ordinal number processing abilities, arithmetic abilities) and domain-general (e.g., working memory capacity, reading ability) behavioral measures. The upshot of such an approach is that it allows for inferences at the level of cognitive mechanisms, examining whether task-based functional connectomes are predictive of similar or distinct sets of cognitive-behavioral outcomes and, thus, whether the tasks are processed by similar or distinct mechanisms. Although a limited number of studies have begun to identify the neural correlates of numerical order processing in children (e.g., Kaufmann et al., 2009; Kucian et al., 2011; McCaskey et al., 2017; Matejko, Hutchinson, & Ansari, 2019; Sommerauer et al., 2020) and adults (e.g., Franklin & Jonides, 2009; Lyons & Beilock, 2013; Attout et al., 2014; Knops & Willmes, 2014), the novelty of Paper IV lies in the attempt to reconcile these two levels of

analysis in a sample of thirty-seven children between the ages of 10–12 years. With these aspects in mind, we hypothesized that the two number processing systems would be dissociable and, as such, produce dissimilar task-based functional connectomes that differ in their predictability of cognitive-behavioral outcome measures. In particular, we reasoned that the functional connectome associated with symbolic ordinal number processing would exhibit stronger predictability of arithmetic outcome measures than that associated with cardinal magnitude discrimination (cf. Lyons et al., 2014).

4.4.2. Methods

The same thirty-seven ($N = 37$) children described for Paper III participated in the analyses for Paper IV (*Mean age* = 11.41; *SD* = 0.55; 12 girls and 25 boys). As previously described, all participants were neurotypical, in good health, and had no clinical or self-reported deficits in either general cognitive ability or mathematics. All participants were right-handed.

The Arabic digit comparison task described for Papers I–III was utilized as a measure of symbolic cardinal magnitude discrimination ability. The same letter case control task (see section 3.3.2), used in Papers I–III, was also administered. Novel to Paper IV was the inclusion of two additional tasks. The symbolic ordinal number processing task consisted of Arabic digit triplets (e.g., 1-2-3), requesting participants to indicate whether the three digits were presented in a correct ascending or descending order, or whether the stimuli were in a mixed order (e.g., 1-5-3) that neither ascended nor descended correctly. Similar to the symbolic cardinal number discrimination task, the numerical ordering task featured near and far-distance trials such that the inter-digit distance within the triplets was either 1 (near; e.g., 5-4-3) or 2–3 (far; e.g., 2–4–6). Participants were instructed to respond to correctly ordered trials, regardless of distance or direction, using the right middle finger (right) response pad button, and to incorrectly ordered trials with a (left) response button placed beneath their right index finger. A symbolic congruity comparison control task was also adminis-

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tered (see section 3.3.2), requiring participants to indicate whether three horizontally presented symbols were congruent (e.g., A-A-A) or incongruent (e.g., 2-B-2). In order to match the response requirements to the corresponding experimental task, congruent trials were responded to with the right-lateralized response button whereas incongruent trials were indicated by the left-lateralized response button. Numerical and alphabetical stimuli were used, both separately (e.g., B-B-B; 4-4-4) and combined (e.g., R-2-R), but different letters or numbers were never used within a trial as to avoid suggesting an underlying ordinal sequence. As described for Papers I–III, each task block featured 14 trials for a total of 84 trials per task (i.e., 14 trials per block $\times$ 2 block iterations per EPI run $\times$ 3 EPI runs). See Figure 1 for an overview of the experimental tasks.

Fifteen behavioral measures were collected as part of a behavioral testing session completed by each participant, prior to neuroimaging data acquisition. In brief, these measures included participant age; arithmetic calculation ability, arithmetic fact retrieval (addition, subtraction, and multiplication), and arithmetic equation scores; response times for the symbolic cardinal number discrimination, nonsymbolic magnitude discrimination, and symbolic ordinal number, alphabet, and nonsymbolic line segment processing tasks; verbal and visuospatial working memory scores; and a measure of reading ability. For a complete overview of tasks, see section 3.3.1 and the Supplementary Materials for Paper IV.

Functional magnetic resonance imaging data were preprocessed using the CONN functional connectivity toolbox version 20.b (Whitfield-Gabrieli & Nieto-Castanon, 2012). Near and far-distance trials were collapsed into single “cardinal” and “ordinal” conditions. Univariate analyses, meaning those targeting the neural correlates associated with either experimental task, were performed in SPM12 (Wellcome Department of Cognitive Neurology, London, UK) and the Statistical Nonparametric Mapping (SnPM version 13.1.08; <http://niso.org/Software/SnPM13/>) toolbox. For this purpose, three statistical

contrast analyses were performed using one-sample T-tests. Two statistical contrasts were employed to identify the unique activity associated with the cardinal (i.e., [Cardinal > Ordinal]) and ordinal (i.e., [Ordinal > Cardinal]) tasks, subtracting activity specific to the opposite task. A conjunction analysis was performed to determine the overlap in neural correlates recruited across both cardinal magnitude discrimination and numerical order processing, subtracted by their respective control tasks (i.e., [Cardinal > Control_{Letter}] $\cap$ [Ordinal > Control_{Congruity}]).

The brain-behavior analyses were performed using *connectome-based predictive modeling* (CPM; e.g., Shen et al., 2017). Task-based fMRI data were imported into a region of interest-based functional connectivity analysis (fcMRI), resulting in subject-specific whole-brain connectivity matrices based on the Shen 268 node parcellation atlas (i.e., 268×268 ROI-to-ROI connections; Shen et al., 2013). These connectivity matrices were collapsed into a $268 \times 268 \times 36$ fcMRI matrix, representing all participants. The association (Spearman's *rho* correlation) between ROI-ROI connectivity values and behavioral outcome measures was investigated, for a total of 30 independent CPM analyses (i.e., 15 behavioral measures $\times$ 2 fcMRI matrices). Leave-one-subject-out cross-validation was performed, such that each subject once constituted the test set (i.e., validating whether patterns observed during training translate to a previously unseen individual) and remaining participants were used to train the classifier. This process was repeated 1000 times with randomized shuffling of behavioral data, to ensure that associations between functional connectivity patterns and behavioral outcome scores did not arise by chance.

4.4.3. Results and Discussion

A Spearman's *rho* correlation analysis (r_s) of the included behavioral measures indicated several statistically significant correlations. Participant age was found to negatively correlate with cardinal magnitude discrimination and nonsymbolic ordinal processing response times. The former—in particular—aligns with

prior research indicating substantial developmental gains in number discrimination ability at ages 10–12 (Papers II–III; cf. Lyons et al., 2014). Arithmetic calculation scores were positively correlated with arithmetic equation scores and visuospatial working memory span. Arithmetic fluency scores demonstrated a positive correlation with arithmetic equation scores, reading ability, and were negatively correlated with all response time measures of number processing—particularly so with regards to ordinal number processing, as hypothesized. Arithmetic equation scores were positively correlated with verbal working memory span and reading scores. Whereas cardinal number discrimination was observed to positively correlate with all other response time-based measures of number processing ability, nonsymbolic magnitude discrimination did not significantly correlate with the ordinal tasks. This outcome suggests a meaningful distinction between symbolic and nonsymbolic number discrimination, where the former may be of greater importance to the development of general numerical and arithmetic abilities (e.g., Lyons et al., 2014). It is also noteworthy that—in contrast to CPM analyses—no domain-general measures (e.g., working memory) correlated with number processing response time measures.

Univariate neuroimaging results indicated shared activity across the cardinal and ordinal number processing tasks in the visual cortex, as well as in the left supramarginal gyrus. Such an activity pattern is indicative of visual processing of numerical stimuli and a maintenance of quantity representations in working memory (e.g., Grabner et al., 2007; Park, Li, & Brannon, 2014; Iuculano, Padmanabhan, & Menon, 2018; Goffaux et al., 2012). It should also be noted that the left supramarginal gyrus constitutes a key node of the perisylvian language network (e.g., Hertrich, Dietrich, & Ackermann, 2020), in support of the hypothesis that cardinal and ordinal number processing systems primarily interface through linguistic abilities (Rubinsten & Sury, 2011).

Activity uniquely elicited by the symbolic ordinal number processing task demonstrated a striking similarity with prior results in adults (Lyons & Beilock, 2013), indicating recruitment of the central executive network (CEN; Bressler &

4 (four, ●●●). *Summary of papers*

Menon, 2010) and the tightly integrated working memory circuit (e.g., Habas, 2021). This interpretation converges with observed activity in the IPS (a key correlate of the CEN), pre-SMA (implicated in sequential order processing; Leek et al., 2016), precentral gyrus (hypothesized to facilitate retrieval from proceduralized count-lists), and the cerebellar vermis associated with the working memory circuit (cf. Lyons & Beilock, 2013; Habas, 2021). The unique activation of the IPS for numerical order processing was unexpected, given the region's purported role in mapping numerical representations to the ANS regardless of task type (cf. Holloway et al., 2013). Two candidate explanations for this outcome are proposed, pertaining to cognitive demand and the role of the IPS in numerical cognition. The first explanation hinges on the notion that a substantial increase in central executive demand for the numerical ordering task—as evidenced by longer response times and lower accuracy—masks IPS activity elicited by the cardinal number discrimination task. The second explanation suggests that the IPS does not map numerical representations to the ANS (as argued by the triple code model), but rather tracks and processes ordinal associations between perceived stimuli (Goffin, 2019). This view has received some empirical support (e.g., Attout et al., 2014), but demands further research in light of conflicting findings (Goffin et al., 2020).

Activity elicited by the symbolic cardinal number processing task demonstrated general agreement with prior accounts of a frontoparietal number network (e.g., Fias et al., 2013), absent the purportedly crucial involvement of the IPS. In contrast to the symbolic ordinal number processing task, the observed neural correlates indicate an increased reliance on the stimulus-driven ventral attention network (VAN; e.g., Corbetta & Shulman, 2002). Recruitment of the right SMG, IFG, and insula—key nodes of the VAN—suggests stimulus-elicited spontaneous item–item comparisons as opposed to top-down, associative chaining based on sequence processing and language-based retrieval (cf. Eger et al., 2003; Piazza et al., 2004; Holloway et al., 2013).

In summary, univariate neuroimaging results indicate distinct patterns of activity for numerical magnitude and order processing. The two tasks indicate a shared reliance on visuospatial working memory, in agreement with the existence of a mental number line. The deployment of visuospatial working memory appears to qualitatively differ across tasks, where numerical order processing requires an integration of verbal and sequential knowledge together with the spatial attention required for retrieval from verbal working memory (Rasoulzadeh et al., 2021). To this end, numerical order processing appears reliant on the central executive network and goal-directed, top-down processing, whereas numerical magnitude discrimination elicits stimulus-driven visuospatial attention to the items' position on the mental number line (e.g., Holloway et al., 2013).

Connectome-based predictive modeling analyses revealed that the functional connectomes, associated with numerical order and magnitude processing, provided distinct predictive capacity for behavioral outcome measures. Notably, the functional connectomes were not cross-predictive, meaning that functional connectivity patterns derived from the ordinal number processing task could not predict performance on the behavioral-level magnitude discrimination task. The same result held in the opposite direction, where the functional connectome derived from the symbolic cardinal number discrimination task was not predictive of response times associated with the behavioral-level symbolic ordinal number processing task. Both task-based connectomes could, however, successfully predict performance on their respective behavioral-level equivalents (i.e., ordinal–ordinal and magnitude–magnitude). This outcome supports the hypothesis of dual number processing systems that build upon dissociable neurocognitive mechanisms, which may also become individually impaired (Rubinsten & Sury, 2011).

Visuospatial working memory capacity was the only behavioral outcome measure successfully predicted by both functional connectomes, aligning with univariate activity-based neural correlate analyses. Thus, the mental number line—supported by visuospatial working memory—appears to provide a common

4 (four, ●●●). Summary of papers

foundation for numerical magnitude and order processing (cf. Morsanyi, O'Mahony, & McCormack, 2017), solidified by prior research demonstrating the importance of visuospatial working memory for the development of number processing and arithmetic abilities (e.g., Ashkenazi et al., 2013; Fanari, Meloni, & Massidda, 2019; Matejko & Ansari, 2021).

Concordant with prior research on the importance of numerical ordering capabilities for arithmetic proficiency (e.g., Lyons et al., 2014), the functional connectome derived from the symbolic ordinal number processing task uniquely predicted arithmetic subtraction fluency scores. This outcome partially aligns with recently published research by Lynn, Wilkey, and Price (2021), demonstrating that symbolic—but not nonsymbolic—number processing tasks uniquely predict math ability in nine-year-old children. Although Paper IV failed to identify predictability of math ability for symbolic discrimination tasks, it appears that symbolic ordering abilities better explain predictive variance in later childhood. Together with unique predictability of participant age (on the order of months), this result indicates a critical developmental period for the refinement of numerical ordering skills and mathematical cognition between 10 to 12 years of age. Key predictive nodes in the right insula, basal ganglia, and cerebellum suggest that the maturation of executive functioning may allow for greater dependence on associative chaining—important for both arithmetic and numerical ordering—as opposed to taxing item–item comparisons, resulting in efficient numerical decisions based on retrieval rather than explicit counting (e.g., Cho et al., 2012; Supekar et al., 2013; Arsalidou et al., 2018).

The identified predictive network nodes indicated large-scale interactions between subcortical, corticostriatal, and cerebellar networks together with neocortical (e.g., frontoparietal) networks more commonly linked to numerical cognition. These network nodes may constitute valuable biomarkers for future explorations of numerical abilities.

5. General discussion

The purpose of this thesis is to increase our understanding of how the neurotypical child and adult brain perceives and processes numerical information. In support of this aim, three principal research questions were posed: how does the brain process different numerical representations? Is this processing dependent on shared neurocognitive mechanisms or attributable to unique, task and format-dependent cognitive processes? What are the effects of biological and cognitive maturation on numerical processing abilities? The following chapter will serve to summarize the answers to these questions, as informed by both the individual and combined outcomes of Papers I–IV.

Numerical cognition is a complex endeavor, evidenced by its differentiation into evolutionarily inherited and biologically primary abilities, as well as the culturally constructed and biologically secondary applications—such as arithmetic—that govern our everyday lives. Despite this apparent complexity, it is commonly argued that all numerical representations, abilities, and applications fundamentally emerge from the evolutionarily inherited approximate number system—onto which symbolic referents of number are mapped and from which referents gain their meaning (e.g., Dehaene et al., 2003). In other words, a considerable proportion of the numerical cognition literature defines number akin to the famous *duck test*: if it looks like a number and acts as a number, it probably is a number. Two such instances of “duck testing” are particularly common: arguments from the existence of shared distance and ratio effects across numerical representational formats (cf. Piazza & Eger, 2016), and arguments from the joint activation of the intraparietal sulcus (IPS) across number codes, species, experimental tasks, or even in the absence of task demands (cf. Dehaene et al., 2003; Nieder, 2016). Together, these examples highlight significant commonalities in the processing of different numerical representations, and indeed provide credible evidence for the notion that these representations all instantiate the same

semantic core concept of *number*. However, the findings of this thesis question the accuracy of this notion, as follows.

5.1. Main findings

A systematic evaluation of the neural substrates associated with numerical cognition, across all three representational codes outlined by the triple code model (TCM; e.g., Dehaene, 1992; Dehaene & Cohen, 1995), was undertaken in Papers I–III. Together, **Papers I–III** indicate that the processing of nonsymbolic and symbolic numbers becomes disentangled over the course of development (cf. Lyons & Beilock, 2018; Marinova & Reynvoet, 2020; Marinova, Sasanguie, & Reynvoet, 2021), such that symbolic numbers gain their semantic reference primarily from other symbolic representations, whereas nonsymbolic numerical magnitude may increasingly be processed in an asemantic and visuospatial fashion. Three main lines of evidence support this position. (1) The neurocognitive overlap between symbolic number processing tasks is greater, in both adults (**Paper I**) and children (**Paper II**), than comparable overlap between nonsymbolic and symbolic number processing. (2) Adults’ increased recruitment of joint linguistic-numerical semantic classification regions (**Paper II**), as well as increased interactions between neural correlates of number processing and the semantic control network (**Paper III**), suggests that symbolic numbers gain distinct semantic content over the course of development. This separation of symbolic and nonsymbolic number processing may occur as early as 10–12 years of age (**Paper IV**), and possibly earlier. (3) Visual and partially asemantic processing of nonsymbolic numerical magnitude appears consistent for adults (**Paper I**) and children (**Paper II**) but may, increasingly, leverage basic visuospatial processing mechanisms as opposed to ANS mapping over the course of development (**Paper III**). Adult-level processing of nonsymbolic numerical magnitude may rather rely on retinotopic maps in the early visual stream, which could be sufficient to discriminate differences in numerical dot arrays (cf. Fornaciai et al., 2017). Typically developed individuals may therefore no longer require the semantic mapping of nonsymbolic numerical magnitude, as supported

by the IPS, but may rather leverage an “asemantic route” with the following properties: visual identification and disambiguation as supported by the occipital cortex (cf. Cavdaroglu, Katz, & Knops, 2015); the resolution of conflict between space and number (e.g., disentangling surface area from numerosity) in the anterior and middle cingulate cortices; and top-down cognitive control over processing strategies, afforded by task demands, in the prefrontal cortex (**Paper I**).

Further probing the symbolic number system, **Paper IV** gives credence to the existence of separate systems for cardinal and ordinal number processing in middle-school-aged children and suggests that the ordinal count-list could be sufficient for establishing symbolic number semantics. This conclusion is primarily based on two lines of evidence: the ordinal number processing task *uniquely* recruits the bilateral IPS, and functional brain connectivity elicited by symbolic numerical ordinality *uniquely* predicts applied symbolic number processing ability as measured by arithmetic fluency. The first line of evidence particularly deserves additional attention given its implications for the field of numerical cognition.

5.1.1. What is the role of the intraparietal sulcus?

The unique recruitment of the IPS during numerical order processing (**Paper IV**) suggests that numerical order is not processed as intermittent magnitude comparisons (i.e., 1-2-3 is deemed correctly ascending by comparing $[1 < 2]$ and $[2 < 3]$), as this activity should not have survived the direct subtraction of *magnitude comparison-specific* activity. This outcome questions whether the IPS is a neural correlate of the ANS, or even specific to number *per se*. Two alternative proposals will be discussed below.

The IPS could be argued to encode ordinal rather than cardinal numerical information (cf. Goffin, 2019; Attout et al., 2014), implying that the IPS activity elicited exclusively by symbolic number comparison tasks (**Paper I**) is the result of

order comparisons rather than magnitude comparisons. The migration of number processing from prefrontal to parietal areas over the course of development (Ansari et al., 2005) may be due to the maturation of cognitive mechanisms allowing for ordinal number processing (cf. Lyons et al., 2014), as suggested by **Paper IV**. In other words, determining the numerically greater alternative out of two number symbols could plausibly leverage an understanding of the count-list (i.e., “which number comes before the other?”), as opposed to a mapping against the mental number line. Rather than being an asemaantic comparison due to its independence from the analog magnitude code and mental number line (cf. Dehaene, 1992), the semantic content could be argued to emerge from the syntactic understanding of the count-list itself.

A second proposal regarding the role of the IPS in numerical cognition, that I personally favor as a result of compiling the results of Papers I–IV, targets executive functions. To some degree, each of the Papers provides hypothetical explanations for possible interference effects between the letter case discrimination control task and the number comparison tasks. This initially appeared to indicate a mismatched control task, arguably subtracting either *magnitude-related* (i.e., mere size differences in lower- and uppercase letters suffice to make a spatial magnitude discrimination in line with ATOM; Walsh, 2003) or *ordinality-related* (i.e., salient alphabetical order cues in letter stimuli eclipse the ordinal aspects of number pairs; cf. Previtali, de Hevia, & Girelli, 2009) activity and resulted in the conspicuous absence of (primarily left) IPS activation across studies. That is, if symbolic number comparison is performed as a “pure” magnitude comparison, spatial magnitude associated with the size of letter stimuli could elicit a similar comparative process. On the other hand, if symbolic number comparison is rather performed in an ordinal fashion, the alphabetical order inherent to letter stimuli could potentially mask similar ordinal number processing in the IPS. However, an alternative explanation based on executive function parsimoniously integrates both of these perspectives *and* the modulation of IPS activation elicited by the neural distance effect (e.g., Holloway & Ansari, 2010). The following section will serve to outline this proposal in detail.

5.1.2. Towards a reinterpretation of the IPS for number

The approximately thirty years of advancements in cognitive neuroscience, since the introduction of the triple code model (Dehaene, 1992; Dehaene & Cohen, 1995), have substantially altered our conception of the brain's modularity. While early neuroimaging research emphasized the discovery of neural modules corresponding to specific behavioral characteristics (e.g., the IPS as implementing magnitude processing), the brain is increasingly characterized as a complex, dynamic, and interactive system where functional networks—rather than functional regions—give rise to cognition. One such functional network is the *central executive network* (CEN), spanning regions such as the bilateral IPS, dorsomedial as well as dorso- and ventrolateral prefrontal cortices, caudate nuclei, and the anterior thalamus (Bressler & Menon, 2010). This network is characterized by its recruitment in tasks featuring high attentional loads, an increased need for cognitive control, and tasks that tax working memory. I argue that the recruitment of the IPS in numerical cognition may precisely reflect such effects of attentional and working memory load, rather than numerosity mappings or a mental number line (cf. Núñez, 2011).

Consider three key findings: (1) the joint activation of the IPS for near-distance number comparisons across formats and participant age-groups (**Papers I and II**); (2) the unique activation of the IPS for numerical ordinality as compared to numerical magnitude in children (**Paper IV**); (3) and the absence of right IPS activity (**Paper I**) and functional connectivity (**Paper III**) during adult-level nonsymbolic magnitude comparison. Finding (1) suggests that IPS activity is most consistently elicited as a function of numerical distance (cf. Holloway & Ansari, 2010; De Smedt, Holloway, & Ansari, 2011), and therefore potentially a measure of increased effort attributable to manipulation of closely related mental representations held in working memory. Finding (2) extends this argument, given that identical Arabic digit stimuli result in significantly different recruitment of neural substrates depending on *what the task demands* participants to do with these digits. Response time and accuracy data suggest that numerical

ordering is significantly more difficult than numerical magnitude discrimination (**Paper IV**), again indicating that IPS activity may be a function of increased attentional and (visuospatial) working memory load. This position is consistent with evidence showing that activity throughout the inferior parietal lobule (including the IPS and AG) generally increases in delayed match-to-sample paradigms (e.g., determining the spatial position of multiple previously observed objects), whereas learned rule-guided decision-making (e.g., determining the larger number) rather elicits activity in a temporoparietal default mode network (cf. Smallwood et al., 2021) similar to that identified in **Paper IV**. That is, the activity-increase attributed to ordinality in the IPS is indicative of visuospatial demands inherent to the demanding ordering and tracking of associations between multiple digits, whereas the cardinal discrimination of only two digits may rather leverage basic schema-based ordering strategies (e.g., “is 3 before 7 in the count-list?”) supported by the default mode network (cf. Vatansever, Menon, & Stamatakis, 2017). Finally, finding (3) suggests that the proposed asemanic visuospatial processing of numerical dot arrays (particularly in adults) poses such a low degree of attentional and executive functioning demands that the involvement of the CEN is effectively minimal. Such an explanation appears consistent with the argument that symbolic numbers are processed in an ordinal rather than cardinal fashion, as evidenced by their unique recruitment of the IPS regardless of numerical distance (**Paper I**).

5.1.3. IPS responds to numerosity in the absence of tasks

A significant caveat to the proposed reinterpretation of the IPS in numerical cognition is found in results by Harvey and colleagues (Harvey et al., 2013; Harvey & Dumoulin, 2017). With the aid of high-field (7 Tesla) fMRI, the mere presentation of different nonsymbolic numerosities (1–7 and 20 dots) was observed to elicit distinguishable neural responses across the posterior parietal cortex. Notably, this was the case despite an absence of tasks (i.e., not attributable to task-induced effort) and when controlling for confounds such as surface area, stimulus size and circumference, density, and stimulus shape. Results indicated that discrete neuronal populations encode specific numerosities, that

larger numerosities are represented more coarsely than smaller numerosities (in line with the logarithmic MNL account), and that neuronal populations tuned to smaller numerosities occupy a greater cortical surface area than those for larger numerosities. Together, this indicates that regions proximal to the IPS contain numerosity maps that particularly respond to specific quantities, albeit predominantly within the subitizing range.

While it is difficult to reconcile the idea that the IPS responds primarily to effort (as induced by increased attentional and visuospatial working memory load) rather than numerosity, in light of these findings of numerosity-selective neuronal populations, I argue that these proposals do not necessarily disagree. Harvey and Dumoulin (2017) argue that the processing of greater numerosities “depends less on attention” (p. 6) than smaller numerosities, which could be taken to indicate that the individuation of objects in the subitizing range (i.e., approximately 1–4) is either more effortful or, at least, relies more on visuospatial tracking and working memory maintenance. Indeed, the authors acknowledge that neuronal numerosity preferences were rare beyond five dots and demonstrated that, during the presentation of 20 dots, number-selective BOLD response amplitudes near the IPS drop to zero. In Papers I–III, a minimum of 8 dots (ranging from 8–26) were presented, which may potentially leverage different neurocognitive mechanisms (and perhaps a more spatially but not attentionally oriented heuristic) than number processing in and closely adjacent to the subitizing range. In this sense, to the extent that the IPS processes number, it could primarily be invoked for the object tracking system (i.e., within the subitizing range) rather than the ANS. Such a conception would align with the proposed “asemantic route” of nonsymbolic numerical magnitude processing beyond the subitizing range, as outlined above. On a final note, the authors did not find number-selective neurons in the IPS *per se* (rather surrounding the post-central sulcus) and, as argued by Harvey and Dumoulin (2017), it may be the case that—for large-quantity approximate number comparisons—actual “IPS ac-

tivation probably reflects responses to comparison tasks [...] rather than numerosity” (p. 7). That is, comparative operations may suffice to elicit IPS activity as opposed to such activity being strictly attributable to the numerical content.

5.1.4. Numerical cognition and executive functions

At the time of writing, a recently published study appears to corroborate the position outlined above. Comparing the neurocognitive mechanisms supporting visuospatial working memory and arithmetic in children and adults, Matejko and Ansari (2021) found a joint left-lateralized frontoparietal network for both tasks in adult participants. Two key findings are of particular relevance to this thesis. First, a conjunction analysis of neural regions common to both arithmetic and visuospatial working memory in adults demonstrated overlapping IPS activation with the parametric (i.e., effortful near-distance) conjunction contrast, across representational codes and age-groups, in **Paper II**. Second, Matejko and Ansari found that visuospatial working memory and arithmetic jointly elicited activity in the right insula, which **Paper IV** indicates to be a key functional node for neurocognitive maturation effects attributable to the development of ordinal number processing and arithmetic. Notably, such joint insula activity was absent in child participants, ranging from 7.7 to 10.4 years of age. This outcome strengthens the proposal that, at approximately 10–12 years of age (Paper IV *participant mean age* = 11.41), neurodevelopmental maturation effects serve to disentangle numerical order and magnitude—and possibly also the way in which nonsymbolic and symbolic numbers gain their semantic reference. That is, once “numerical maturation” occurs, symbolic numbers may increasingly leverage visuospatial working memory to store and manipulate numerical information for comparison with semantic memory cues of the ordinal count-list or arithmetic facts. One prominent role of the insula concerns its coordination between the central executive and default mode networks, such that it moderates the switching between resting-state (default mode) and task-focused (multiple-demand, frontoparietal) neural functional connectivity (e.g., Uddin et al., 2017). In this sense, maturation of the insula can be argued to provide a foundation for the executive functions required to successfully engage with attentionally and

executively demanding tasks, such as symbolic arithmetic or numerical order processing (cf. Ashkenazi et al., 2013).

This proposal aligns with several key findings derived from adults' functional number network connectivity, across the symbolic codes, in **Paper III**. The right middle frontal gyrus and adjoining inferior frontal sulcus—together with the IPS—constitute key nodes of the multiple demand (and frontoparietal) network, elicited by cognitively taxing tasks (e.g., Duncan, 2010). The IFS and IPS are important hubs for discriminating context information during task processing, rendering them crucial for top-down goal-directed attention, and have thus been argued to comprise components of an executive cognitive control network (Waskom et al., 2014). Their consistent interconnectivity—through left hippocampus multiple-item working memory—for adult-level symbolic number processing indicates that typical maturation allows for increased cognitive control, supporting efficient online integration of symbolic knowledge in the MTL memory system (cf. Duff et al., 2020), left SMG and right hippocampus (for Arabic digits), and the left MTG (for verbal representations of number) together with IPS-supported visuospatial working memory processing. The default mode network (here characterized by the hippocampus and MTG) has furthermore been observed to contribute to both semantic retrieval and the maintenance of goal representations in working memory (Wang et al., 2021), lending additional support to the interaction of visuospatial working memory, cognitive control, and semantic retrieval as cornerstones of adult symbolic number processing.

Appealing to executive functions and attention as central to the typical development of numerical cognition is not a novel idea, although the results of Papers I–IV could be argued to strengthen the empirical evidence for such a position. Ashkenazi and Henik (2010) argue that “pure” (i.e., non-comorbid with dyslexia or ADHD) developmental dyscalculia is characterized by additional deficits in attention and executive functions, with reference to studies advocating similar positions as early as the turn of the twenty-first century (e.g., Bull & Scerif,

2001; Wilson & Swanson, 2001). Thus, the successful acquisition and deployment of number may fundamentally depend on the integrity of the central executive network (featuring the IPS as a key node) and its capacity to interact with the semantic control and retrieval networks (cf. Sommerauer et al., 2020), as moderated by the insula’s task-appropriate distribution of neurocognitive resources in the salience network.

5.2. P versus A-conscious Number processing model

In order to summarize the results of this thesis, a tentative model with testable predictions may fruitfully be specified for examination and validation by future research. Drawing on the central neural correlates of number processing identified in Papers I–IV, the aim of this model is to align patterns of neural activity, functional connectivity, and key research findings both within and beyond the field of numerical cognition. The proposed name for this model, *P versus A-conscious Number processing* (PAN), mirrors recent calls for disambiguating the discrete, cardinal, and symbolic instances of number on the one hand, and the processing of approximate, continuous, and *quantical* (cf. Nùñez, 2017) numerical information on the other hand (e.g., Sokolowski et al., 2021).

The PAN model takes its primary inspiration from Block’s (e.g., 2008) distinction between *phenomenal* (P) and *cognitive access* (A) consciousness. At its core, the distinction between these two states of conscious processing lies in (what I consider to be) semantic content-awareness. Phenomenal perceptions (e.g., basic awareness of low-level visual properties such as luminance) are noticeable but feature limited cognitive accessibility, leading to difficulties in accurately reporting the content of the perception. Cognitively accessible perceptions (e.g., conscious disentanglement of words and colors in a typical Stroop task), on the other hand, can be characterized by a necessarily deeper cognitive level of engagement as a means of semantic interpretation, leading to a higher degree of reportability. This entails that the cognitively accessible content needs

to be maintained in working memory, in order to interface with top-down attention and long-term memory retrieval. Consider the following example: when asking a participant why he or she chose “7” as opposed to “3” as the numerically greater alternative, responses can appeal to principles of cardinality (i.e., countability) or ordinality (i.e., sequential positional value). Without explicit counting, the same cannot be said for large-quantity nonsymbolic numerical dot arrays. Participants would likely rather appeal to visual cues (e.g., surface area) or a more intangible *feeling*—informed by their ANS acuity and ability to perceive differences in magnitude—that either array contained more or less objects. Thus, the more a perceived numerical representation demands a content-aware semantic interpretation, the more it is processed in a cognitively as opposed to phenomenally driven fashion. Extending this reasoning, more complex instances of symbolic number processing (e.g., ordinal processing tasks or arithmetic) would fall further along the cognitive (A) side of the phenomenal–cognitive access continuum (see Figure 3) as a function of increased task demands, working memory involvement, and semantic interpretation of symbolic referents.

Considering human numerical cognition on a continuum, ranging from phenomenal to cognitively accessible processing, the results of Papers I–IV begin to paint a coherent picture. Large-quantity nonsymbolic representations of number (i.e., beyond the subitizing range) possess a degree of visual complexity that *overflows* visuospatial working memory capacity. While individual differences exist for visuospatial working memory capacity, group-level averages tend to suggest a stable upper encoding limit of approximately three objects in set sizes ranging from four to eight objects (e.g., Todd & Marois, 2005). This aligns with previously described results by Harvey and Dumoulin (2017), showing that IPS-adjacent and putatively quantity tracking-specific neural activity decreases above five objects. Thus, while a large-quantity numerical dot array may be stored in short-term visual iconic memory and remains accessible during the subsequent numerical discrimination process, it is represented with low content-awareness. In other words, a coarse visuospatial and phenomenal summary

representation of approximate numerosity persists in consciousness, but each individual object (e.g., dot) is not available for content-aware cognitive access (cf. Block, 2011). This may explain why adults, as a means of task-appropriate cognitive flexibility, only uniquely recruit the cognitive-control and decision-making processes attributed to the anterior cingulate cortex (**Paper II**) in non-symbolic number processing and leverage a seemingly feedforward visuospatial functional network of regions (**Paper III**), as opposed to inefficient counting and cognitive access-based strategies.

Figure 3. The phenomenal–cognitive access continuum and relative placement of different numerical representational formats. Dashed line indicates the (visuospatial) working memory limit, where the area to the left indicates overflowed capacity (cf. Block, 2008).

Symbolic number processing, on the other hand, does not overflow working memory capacity within the numerical ranges studied in this thesis (i.e., two concurrent digits or number words and Arabic digit triplets). This entails that the entire perceptual content of a symbolic number processing task can be cognitively accessed (cf. Block, 2011), prompting the interaction between content in working memory, task-modulated top-down attention, and semantic retrieval of relevant numerical facts in the decision-making process. Examining the developmental differences in neural activity (**Paper II**) and functional connectivity (**Paper III**), symbolic number processing tasks appear to increasingly require a distributed neurocognitive feedback loop between substrates of executive function and attention (e.g., IPS, MFG, IFG), cognitive control (e.g., ACC, MCC), and semantic retrieval (e.g., SMG, MTG, hippocampus). That is, as opposed to the feedforward visuospatial processing of nonsymbolic number, symbolic instances of number processing give rise to content-aware “global ignition” (cf. Mashour et al., 2020)—transitory widespread increases in global brain activation and functional connectivity—eliciting distributed domain-general cognitive processing (see Figure 4). To reach adult-level maturity, neurocognitive development primarily affects the MTL memory system (**Paper III**) necessary for semantic retrieval, as well as the basal ganglia (e.g., caudate nucleus, thalamus), salience and cingulo-opercular (e.g., insula, ACC) networks required for working memory and task-relevant distribution of cognitive resources necessary for content-aware cognitive access (**Paper IV**; cf. Fias et al., 2013). The results of **Paper IV** suggest that this pattern scales with the semantic complexity of the task, where symbolic ordinal number processing (requiring the tracking of multiple digits, their interrelationships, and accessing their meaning) biases neurocognitive processing further into the cognitive access end of the phenomenal–cognitive access continuum.

Figure 4. Extending the PAN model with central neural correlates of number processing. Dashed line indicates the (visuospatial) working memory capacity limit. Left: nonsymbolic number discrimination. Middle: symbolic number discrimination. Right: key child symbolic ordinality processing regions. Red: neural activity. Green: patterns of functional connectivity (left and middle: adult-level functional connectivity; right: functional connectivity predictive of neurodevelopmental maturation). VM-/VLPFC: ventromedial/-lateral prefrontal cortex. ACC: anterior cingulate cortex. MCC: middle cingulate cortex. MFG: middle frontal gyrus. PMc: premotor cortex. SPL: superior parietal lobe. IPS: intraparietal sulcus. SMG: supramarginal gyrus. MTG: middle temporal gyrus. HC: hippocampus. CN: caudate nucleus. FG: fusiform gyrus. CB: cerebellum. BG: basal ganglia.

The PAN model should be interpreted as a dynamic system-view of neurocognitive function, where functional constellations of neural substrates modulate their behavior in line with necessary semantic content-awareness (i.e., conscious cognitive processing) elicited by task demands. As such, the model places less emphasis on individual neural correlates corresponding to putative cognitive functions, but rather on how overall patterns of activity and functional connectivity converge to make numerical representations cognitively accessible for domain-general processing mechanisms. In this vein, the placement of different numerical representational formats along the phenomenal–cognitive access continuum is not static, but rather dependent on the task at hand. In a typical naturalistic scenario (e.g., when choosing the shortest queue at the supermarket), nonsymbolic representations of quantity are likely not subject to particularly effortful distance effects, affording a basic and asemantic level of visuospatial processing distinct from symbolic numerical cognition. However, the experimental manipulation of numerical distance can give rise to a task-evoked shift into cognitive accessibility, as the numerical difference between two nonsymbolic dot arrays becomes more difficult to distinguish. While unavailable to the same degree of cognitive access as symbolic representations (partially due to working memory capacity limits), near-distance nonsymbolic comparisons elicit similar task-evoked frontoparietal network activations indicative of effortful and content-aware number discrimination (see Figure 5). This basic semi-content-aware comparison mechanism may help explain why nonsymbolic number processing abilities are predictive of arithmetic outcomes, but less so when controlling for symbolic number processing skills that further afford and demand (increasingly cognitive-aware) semantic symbolic reference (cf. Lyons & Ansari, 2015).

Figure 5. Numerical distance effects show a common shift towards cognitive access (A) processing in both symbolic and nonsymbolic representational formats. Red: key adult-level neural activity clusters. Rose plots indicate intrinsic connectivity network involvement in line with the 20 component (numbers indicate components) brain map (Laird et al., 2011), derived from the ICN Atlas toolbox for SPM12 (Kozák et al., 2017). Task conjunction refers to overlapping activity of experimental tasks subtracted by the control task. Parametric conjunction refers to analysis of [near > far] distance effects. WM: working memory.

The PAN model may be of some explanatory value for future research on numerical and mathematical disabilities, including developmental dyscalculia. Deficit studies often appeal to explanations centered around the IPS, either in terms of differences in (relative to a control group) activation levels, gray matter volume, or functional connectivity (cf. Träff et al., 2017). If it is indeed the case that the IPS primarily instantiates visuospatial working memory and attention, rather than numerosity representations *per se*, a prediction for future research is that deficient numerical cognition universally results in the same type of working memory overflow described for nonsymbolic large-quantity discrimination tasks. That is, the overall threshold for reaching content-aware and cognitively accessible (A) number processing may be increased as a function of deficient regulation of executive function and attention (cf. Ashkenazi & Henik, 2010). A similar argument was put forth by Rotzer and colleagues (2008), finding reduced gray matter volume in the right IPS of dyscalculic children and highlighting the region's involvement in working memory and attention. The outstanding question, as posed by the authors, is thus still “if the frontoparietal network in DD plays a specific, number-related role [...] or has to be considered in a more general way” (Rotzer et al., 2008, p. 420).

5.2.1. Future research on the PAN model

Based on the discussion above, three predictions can be advanced based on the three main research questions guiding this thesis. I argue that these predictions can be fruitfully explored in future research on the neurocognitive bases of human number processing.

(1) How does the brain process different numerical representations?

The PAN model predicts that nonsymbolic and symbolic numbers are conceptually distinct and are processed increasingly independently of each other over developmental time. Nonsymbolic number processing in the subitizing range (as supported by the OTS) may share commonalities with symbolic number processing—and even aid in the establishment of symbolic count-list semantics—given that a limited number of objects permit content-aware cognitive access in

visuospatial working memory. This aligns with findings by Bulthé and colleagues (2015), demonstrating that IPS activity corresponds better to the number of perceived objects as opposed to numerical content. That is, the representational overlap between a single dot and digit is greater than that between a number of dots and their associated symbolic referent, suggesting that the IPS responds to number in the subitizing range—not necessarily as a function of *number*, but in the sense of domain-independent object tracking for visuospatial working memory maintenance. Large-quantity nonsymbolic number processing (as supported by the ANS) overflows working memory capacity, resulting in primarily asemantic (phenomenal) visuospatial feedforward processing supported by cognitive control (e.g., ACC) and mechanisms implicated in mental rotation and motor imagery (e.g., left precentral gyrus). Symbolic representations of number necessarily require semantic interpretation (cognitive access), leading to an increased reliance on feedback loops between working memory and top-down attention control (e.g., IPS, MFG), semantic memory (e.g., hippocampus), and lexico-semantic processing regions (e.g., SMG, MTG). Cognitive access to numerical content is further enhanced by ordinal processing tasks, necessitating high domain-general content-awareness in order to retrieve numerical facts and manipulate the order of a given digit triplet in line with the lexico-semantic count-list.

(2) Is this processing dependent on shared neurocognitive mechanisms or attributable to unique, task and format-dependent cognitive processes? In broad terms, the distinction between nonsymbolic and symbolic number processing can be characterized in line with the two-streams hypothesis (e.g., Milner & Goodale, 2008): nonsymbolic number processing is performed primarily in the dorsal *vision-for-action* stream (i.e., visuospatial “where” processing), whereas symbolic number processing rather leverages the ventral *vision-for-perception* stream (i.e., object-based “what” recognition). This distinction corresponds well to the PAN model’s conception of phenomenal and cognitively accessible number processing, where the former allows for asemantic and perceptually straightforward approximations of number (or other

general magnitudes such as space and time; e.g., Walsh, 2003) for instantaneous motor action, whereas the latter requires access to culturally and linguistically informed semantic facts. These mechanisms appear to operate independently of one another, save for a common reliance on visuospatial working memory and attention.

(3) What are the effects of biological and cognitive maturation on numerical processing abilities? While verbal number discrimination stands out due to its unique perisylvian language network maturation effects (**Paper II**), the PAN argues that biological and cognitive maturation supportive of number processing and arithmetic primarily takes place in the basal ganglia, MTL memory system, as well as salience and cingulo-opercular networks (**Papers II–IV**). Generally, this developmental pattern appears to support the view that executive function (including working memory), attention, and task-appropriate cognitive strategy use (e.g., the adoption of associative chaining as opposed to item–item comparison mechanisms) begin to emerge during a crucial neurodevelopmental maturation period, around 10–12 years of age. Concurrently, this maturation allows for improved symbolic number ordering capabilities and arithmetic ability. A possible interpretation is that the task-appropriate switching between task-positive (e.g., multiple demand, central executive, frontoparietal, and semantic control) and default-mode networks, through the salience network, is subject to considerable maturation effects that lead to significant gains in numerical cognition abilities.

The early-stage outline of the PAN model presented here requires more work and experimental evaluation, although it may constitute a worthwhile starting point for future research in numerical cognition.

5.3. Limitations and future directions

The recent identification of a replication crisis in psychological research (e.g., Open Science Collaboration, 2015) has similarly raised debate about the replicability of neuroimaging research. The lack of standardized methods, analysis pipelines, and statistical software packages (to name a few crucial factors) allows for multiple potential pitfalls in the replicability and generalizability of results derived from functional magnetic resonance imaging data. A review of 241 research reports, utilizing fMRI data, found a total of 207 (i.e., approximately 86%) unique analysis pipelines (Carp, 2012). The analysis of identical datasets across three different statistical analysis software packages for neuroimaging data (AFNI, FSL, and SPM) yielded significant differences in results, with several cross-software comparisons ranging below 50% overlap in obtained statistical maps (Bowring, Maumet, & Nichols, 2019). Moreover, the analysis of a single neuroimaging dataset with nine predefined hypotheses, by 70 independent research teams, indicated that all teams not only used different analysis pipelines but also reported markedly different results (Botvinik-Nezer et al., 2020). The results presented in this thesis are similarly not impervious to such analytical pitfalls and will require future replication and validation. Ideally, future analysis of the data may be performed with different analysis pipelines and software packages in order to ensure the reliability of results.

For Paper I, it should primarily be noted that the employed exclusion criteria, for high-motion participants, relied on a common but arbitrary threshold of movement greater than 4 mm along any axis. While such an approach provides a coarse filtering of participants, the use of more sophisticated and data-driven exclusion criteria for Papers II–IV yielded considerably different sample characteristics. Paper II adopted the fMRIPrep pipeline (Esteban et al., 2018), designed as a universal best-practice alternative for consistency of results, which particularly reduced the admissible sample of child participants. Given that high motion has been observed to confound functional connectivity in the prefrontal cortex (e.g., Power et al., 2012), coupled with the fact that increased prefrontal

cortex activity has typically differentiated child and adult number processing (e.g., Ansari et al., 2005), it is important to systematically control the effects of motion to ensure that results detail purely cognitive ontogenetic differences. Future replication attempts should particularly investigate if the lack of unique prefrontal activity in children’s number processing (Paper II) is due to maturation effects (cf. Mussolin et al., 2013), or if it may be the case that the pre- and postprocessing pipeline employed by fMRIPrep and fMRIDenoise (Finc et al., 2019) is excessively stringent.

Participating children, in Papers II–IV, can be classified as high-achieving based on the average interpolated Raven’s Standard Progressive Matrices percentile of 75.33 ($SD = 25.56$). Thus, the maturation effects described in this thesis may be partially subject to above-average non-verbal intelligence, which requires further investigation in both performance-matched and average child participant samples.

The results of the current thesis describe a participant sample approximately spanning the ages of 10 and 30. Future research should attempt to widen this age span further, particularly given the observed developmental maturation effects attributable to numerical ordinality and symbolic number processing. The sample size for this thesis falls within the typical range for neuroimaging research on numerical cognition (e.g., Arsalidou & Taylor, 2011), and particularly so for children (cf. Arsalidou et al., 2018), but future research should nevertheless attempt to replicate the current findings with additional participants.

Future studies of developmental differences in number processing would benefit from an additional focus on longitudinal designs. While prohibitively costly and time-demanding within the scope of a PhD candidacy project, the longitudinal tracking of individuals’ numerical and neurocognitive development throughout childhood and adolescence would provide a more fine-grained account than the current cross-sectional design. Nevertheless, the coarse differences identified between age-groups, particularly so in **Paper III**, provide a

promising foundation for future research detailing the potential ontogenetic shift from ANS-based to symbol and visuospatial ability-based numerical cognition.

Future research should increasingly apply novel machine-learning tools to investigate both whole-brain and region of interest activation patterns attributable to numerical cognition (cf. Bulthé et al., 2019). For instance, in order to determine the role of the IPS for number processing in a more data-driven manner, support vector machine-based classifiers could be employed in order to investigate whether a classifier: (1) can be trained to identify differences in magnitude across numerical representational codes and whether neural representational differences arise in children and adults; and (2) whether predictability of numerical magnitude or ordinality successfully transfers to activity patterns derived from visuospatial working memory tasks. For the latter question, such analyses could fruitfully investigate potential differences between numerical distances, in order to investigate whether neural ratio effects indicated by IPS activity correspond better to numerical distance or visuospatial working memory load.

5.4. Conclusions

Together, the Papers indicate that the brain processes nonsymbolic (e.g., ●●●) and symbolic (e.g., “3” and “three”) number in qualitatively different fashions. The neurocognitive overlap between symbolic numbers appears greater than corresponding overlap between nonsymbolic and symbolic representations, suggesting that the evolutionarily inherited capacity for numerical magnitude discrimination may—at most—provide a biologically evolved precondition (cf. Núñez, 2017) for the development of symbolic number semantics. As early as 10–12 years of age, and possibly earlier still (cf. Marinova & Reynvoet, 2020), symbolic and nonsymbolic numbers appear to become disentangled entities. This shift may be attributable to the development of adult-level ordinal number processing abilities, in turn supported by a maturation of executive functions

(primarily visuospatial working memory) and the establishment of neural pathways that integrate numerical-linguistic semantics with efficient memory retrieval strategies (e.g., associative chaining). In practice, this could be taken to entail that symbolic numbers are understood in reference to other symbolic numbers (e.g., “2” is “1 more than 1”), as informed by the ordinal count-list (i.e., “1, 2, 3, 4, ...”).

The intraparietal sulcus and its putative specialization for number may be characterized as a “domain-specific end state [stemming from a] more domain-general start state” (Karmiloff-Smith, 2006, p. 9), where the region plays a role specific to numerical cognition by virtue of supporting crucial, domain-general working memory processes. This would align with the generalized magnitude system for space, time, and number (e.g., Buetti & Walsh, 2009), indicating that the IPS serves as a necessary precondition for attentional and working memory demands associated with general magnitude discrimination—not number *per se*. Deficient processing in the IPS may nevertheless also negatively impact numerical cognition, making it “domain-specific” in the sense of being a fundamental neural substrate and functional hub for number processing.

Crucially, the IPS may serve a basic representational role in the encoding of number and numerosity in the subitizing range (cf. Harvey et al., 2013), but likely not in the sense that the region “houses a number module” (Iuculano & Menon, 2018, p. 191). Rather, as argued by Iuculano and Menon (2018), the IPS may be fundamental to numerical cognition by means of supporting “spatial attention, individuation, and pointing of objects in extrapersonal space as well as the encoding of the locations of objects into visual short-term memory storage [... playing] an important role in the individuation of objects in space, thereby contributing to the development of functional systems for the estimation of quantity” (p. 191). In other words, quantity representations in the subitizing range—as supported by the object tracking system—may be encoded by the IPS, serving as a foundation for the visuospatial individuation of objects that later inform the ordinal count-list, in turn giving rise to symbolic number processing

abilities (cf. Le Corre & Carey, 2007). Whether this implies that the IPS fundamentally processes numerosity, or whether it acts more akin to a “working memory storage” of perceived stimuli (e.g., by assigning mental symbols—as position markers—for each stimulus to segment objects from their surroundings), remains to be explored in future research. The question is, thus, whether the IPS semantically represents numerosity itself or if numerosity representations arise as a byproduct of lower-level visuospatial attention and working memory processes, serving to segment complex visual scenes into interpretable, “mentally tagged” constituent parts (cf. Bulthé, De Smedt, & Op de Beeck, 2015).

The identified neural correlates of typical number processing, both in children and adults as well as across different numerical representational formats and tasks, may provide a useful reference for future research on the neurocognitive foundations of number processing. Moreover, these results may act as an important baseline for comparison with deficient numerical cognition.

Numerical education, including arithmetic, may benefit from an increased focus on symbolic numerical abilities and numerical ordinality in particular. Moreover, previously observed gains in general numerical and arithmetic abilities as a result of number line training (e.g., Michels, O’Gorman, & Kucian, 2018) may be due to the successful disentanglement of number and irrelevant domains (e.g., space), serving to increase the acuity of executive functions (cf. Babai, Cohen, & Stavy, 2008). Previously successful interventions for deficient numerical cognition, such as the boardgame *The Great Race* (Ramani, Siegler, & Hitti, 2012), may combine these aspects with the ordinality inherent to moving tokens across numbered squares (e.g., “one, two, three”) in line with instructions (e.g., “move three steps forward”)—rather than targeting the cardinal magnitude aspect of number.

Returning to the initial question posed in the introduction of this thesis, whether nonsymbolic representations of numerical quantity are fundamentally the same

instantiation of number as Arabic digits and number words, the combined empirical evidence and theoretical discussion suggest this to not be the case. While this view stands in contrast to foundational research in the field of numerical cognition, it more so aligns with what I perceive to be an emerging contemporary consensus. Based on the outcomes presented here, I have suggested a tentative first draft of the PAN model. Notably, this model diverges from the triple code model (TCM)—which has served as a central methodological foundation for this thesis—and its tight interdependence between nonsymbolic and symbolic number processing mechanisms and semantic content. I suggest that the field of numerical cognition should increasingly study the neurocognitive mechanisms of lower-level, domain-general cognitive abilities that support the perception and manipulation of numerical information, as semantically represented by and accessible to a dynamic and content-aware functional neural network.

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