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How Do Humans Process Magnitudes? An Examination of the Neural and Cognitive Underpinnings of Symbols, Quantities, and Size in Adults and Children

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Abstract

A striking way that humans differ from other species is our unique ability to represent and manipulate symbols. This ability to process numerical magnitudes symbolically (e.g., ‘three’, ‘3’) is widely thought to be supported by an ancient system that evolved to process nonsymbolic numerical magnitudes (i.e., quantities). In this thesis, I present four empirical studies to uncover whether symbolic representations are indeed supported by the system that evolved to process quantities, or if symbolic representations are sub-served by a similar but ultimately distinct system.

In experiments 1 and 2, I investigate how the adult brain processes symbols and quantities using quantitative neuroimaging meta-analytic techniques (Experiment 1), and a tightly controlled fMRI paradigm (experiment 2). Results from the meta-analysis indicate that symbols and quantities are sub-served by both common and distinct brain regions along the frontal-parietal lobes. However, using a tightly controlled adaptation paradigm to isolate brain regions that underpin symbols and quantities reveal that regions supporting symbols are quite distinct from those supporting quantities, spatially and representationally. Thus, symbols might not be processed using the system that evolved to process quantities.

In experiment 3, I examine whether the processing of symbols is similar to quantities under different attentional conditions. I discover that in addition to participants being more efficient at effortfully comparing symbols than quantities, embedding distracting symbols into stimuli during a quantity comparison task affected performance more than embedding quantities into a symbolic comparison task. This indicates that symbols and quantities are processed differently, under different attentional conditions, and therefore are likely sub-served by different representational systems.

In experiment 4, I investigate the origin of the difference between how humans process symbols and quantities by exploring whether children’s symbolic number knowledge relates to their spontaneous attending to quantities. I find that children are more likely to attend to quantity if they know the number word that corresponds to the quantity, suggesting that learning symbols may influence how children conceptualize quantities.

In summary, while there are some similarities in how humans process symbols and quantities, there are many important differences both behaviourally, and the neural level of organization. Consequently, these findings challenge the longstanding belief that the culturally acquired ability to conceptualize numbers symbolically is grounded in the ancient system that evolved to estimate quantities.

Keywords

Symbolic numerical magnitude, nonsymbolic numerical magnitude, non-numerical magnitude, functional magnetic resonance imaging (fMRI), human uniqueness, cognitive development,

Summary for Lay Audience

The uniquely human ability to think about numbers as symbols sets us apart from other species that can only think about numbers nonsymbolically (i.e., quantities, such as collections of dots). How does the human brain support this exceptional ability to conceptualize numbers symbolically? Are the ancient systems that evolved to estimate quantities repurposed for symbolic thinking? I examine similarities and differences in how humans think about symbolic numbers compared to quantities.

I explore whether the parts of the adult human brain that are activated in response to symbolic numbers are also activated in response to quantities. Specifically, I 1) synthesize previous research that examines brain responses to symbols and quantities to identify consistencies across these studies and 2) collect measures of brain activation while participants passively view symbols, quantities, and physical sizes. I discover that brain regions that are associated with thinking about numbers symbolically are quite distinct from brain regions that evolved to understand quantities.

Subsequently, I examine whether the similarities and differences between thinking about symbols and quantities depend on what participants are instructed to pay attention to. I discover that participants are faster and more accurate, comparing two symbols than two quantities. Additionally, when participants compare quantities, they perform more poorly if there is a distracting symbol present. Interestingly, the presence of a quantity when comparing symbols is less distracting. Together, this work shows that how human adults think about symbols and quantities is quite different.

To understand the origin of this difference I explore the relationship between how humans think about symbols and quantities in children, while these systems are developing. I examine whether having knowledge of symbolic numbers influences the degree to which children notice quantities in their environment. I find that children are more likely to notice and use quantities to solve a problem if they have learned the verbal number word that corresponds to the quantity.

Discoveries from this thesis reveal that humans conceptualize symbolic numbers in a way that is quite distinct from nonsymbolic quantities. This indicates that humans possess a

system used to process symbols that is distinct from the evolutionarily ancient system used to estimate quantities. Future investigations are needed to understand better how we learn numerical symbols over the course of our development.

Co-Authorship Statement

The research for this doctoral thesis was designed and conducted in collaboration with and under the guidance of my advisor Dr. Daniel Ansari. For all studies in this thesis, Dr. Ansari contributed to the design, analysis, interpretation of the findings and preparation of the final manuscript. Chapter 2 was conducted in collaboration with Dr. Wim Fias and Ahmad Mousa. Dr. Fias is contributed to the theoretical ideas for chapter 2 as well as, interpretation of the results. Ahmad Mousa provided assistance coding the neuroimaging studies included in this chapter. Chapter 3 was conducted in collaboration with Zachary Hawes and Dr. Lien Peters, Zachary Hawes significantly added to the theoretical, analytical and experimental aspects of this study. Dr. Lien Peters contributed to the execution and interpretation of the multivariate analyses included in this chapter. Chapter 4 was conducted in collaboration with Zachary Hawes and Dr. Tali Leibovich who both significantly added to theoretical, analytical and experimental aspects of the first and second experiments. Finally, Chapter 5 was conducted in collaboration with Dr. Rebecca Merkley, Sam Kingissepp and Praja Vaikuntharajan. Dr. Merkley was involved in the theoretical, and experimental set-up of this study. Sam Kingissepp and Praja Vaikuntharajan assisted in many aspects of data collection, including scheduling participants, collecting data, and entering data. While all of the material contained in this document is my own work, it must be acknowledged that Dr. Ansari provided assistance editing and revising all of the written material in this thesis.

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Table of Contents

List of Tables

List of Figures

List of Appendices

Chapter 1

1 General Introduction

Contemporary society could not function without numbers. We would be unable to draft architectural plans, calculate the value of a currency, design engines and motors, identify how many calories we need to maintain a healthy weight, or even tabulate votes in a democratic election. Since basic number processing is a cognitive foundation that supports mathematical thinking, understanding the development of the behavioural and neural signatures of number processing provides insight into how the brain manages the critical and distinctly human task of understanding complex math. Moreover, as mathematical ability is a learned skill that builds on related, previously acquired knowledge, the study of numerical and mathematical processing serves as a model for understanding learning more broadly, across multiple domains. The examination of numerical processing also has important practical implications. Indeed, early mathematical competence is the single strongest predictor of later academic achievement and financial stability (Duncan et al., 2007; Romano, Babchishin, Pagani, & Kohen, 2010). At the societal level, improving math scores is tightly linked with cross-national GPD growth (OECD, 2010). In direct contrast, low mathematical ability is related to higher rates of mental and physical illness, unemployment, and incarceration (Bynner & Parsons, 1996; Parsons & Bynner, 2005).

Critically, mathematical performance of Canadian students on international math assessments has been on a steady decline since 2003 (Stokke, 2015). As recently as last year, half of grade 6 students in Ontario failed to meet provincial standards for mathematics (Alphonso, 2018). Thus, the study of the neuropsychological underpinnings of numerical processing is not only intellectually fascinating but also practically relevant – and urgently needed – in understanding and improving the world-wide debilitating effects linked to low math achievement.

In what follows, I will introduce you as the reader to the field of numerical cognition. As such, I will provide a brief overview of dominant theories relating to basic number processing across developmental time. Following this, I will summarize the current state of the field and present outstanding questions. Finally, I will outline the four empirical studies that address these outstanding questions and comprise the body of this thesis. Following the conclusion of chapter 1, the four empirical studies and their results will be described in detail within their own chapters. The thesis will conclude with a sixth chapter that integrates findings from the four empirical studies and outlines future directions for the field of numerical cognition.

1.1 Nonsymbolic Numerical Magnitudes

Humans share with other animals, such as non-human primates, birds, bears, amphibians, and fish, the ability to process the quantities of nonsymbolic numerical magnitudes such as set of objects or an array of dots (For review see: Cantlon, 2012; Dehaene, Dehaene-Lambertz, & Cohen, 1998; Nieder & Miller, 2004). This capacity to estimate and discriminate between nonsymbolic numerical magnitudes often referred to as 'number sense,' has been quantified and delineated across a large body of research (Cantlon, 2012; Dehaene, 2007; Dehaene et al., 1998; Nieder & Dehaene, 2009). This research has revealed that the ability to process nonsymbolic numerical magnitudes is conserved across species (Brannon, 2006; Cantlon, 2012; Dehaene et al., 1998; Nieder & Dehaene, 2009) and that it emerges early in development (Izard, Dehaene-Lambertz, & Dehaene, 2008; Starr, Libertus, & Brannon, 2013; Xu, 2003; Xu, Spelke, & Goddard, 2005). This suggests that the ability to estimate nonsymbolic numerical magnitudes has a long evolutionary history. One potential explanation for the phylogenetic and ontogenetic continuity of this ability, to process nonsymbolic numerical magnitudes, is that the capacity to estimate quantities supports functions that have been and are currently critical for survival, such as identifying regions with an abundance of food or approximating the number of approaching predators (Cantlon, 2012; Geary, Berch, Mann Koepke, 2015; McComb, Packer, & Pusey, 1994; Vonk & Beran, 2012). Critically, it has been suggested that the evolutionarily ancient ability to process nonsymbolic numerical magnitudes may be a necessary element of the foundation that supports the capacity to understand numerical information. However, humans also have developed the ability to represent numbers symbolically.

1.2 Symbolic Numerical Magnitudes

Relatively recently in human history, a broad set of capabilities emerged that resulted in the uniquely human capacity for symbolic abstraction (Ansari, 2008; Coolidge & Overmann, 2012). In view of this, in addition to having an ancient, nonsymbolic ‘number sense’ that is shared among non-human species and emerges early in development, humans have a unique ability to represent numerical magnitudes symbolically such as with the verbal word ‘three’ or the Arabic digit ‘3’ (Ansari, 2007, 2008; Coolidge & Overmann, 2012; Kersey & Cantlon, 2017; Núñez, 2017). In direct contrast to the evolutionarily ancient system that evolved to support the processing of nonsymbolic numerical magnitudes, the uniquely human capacity to represent numbers symbolically emerged as a result of enculturation (Ansari, 2008; Núñez, 2017). This culturally acquired capacity to understand and manipulate symbolic numerical magnitudes is foundational for later, more advanced mathematical abilities (De Smedt, Noël, Gilmore, & Ansari, 2013).

The striking way that humans differ from non-human animals in our ability to represent and process numerical magnitudes symbolically is undoubtedly a core element of our unique human capacity for higher-level mathematical thinking. A key question in the field of numerical cognition has been whether the ancient system(s) that evolved to process nonsymbolic numerical magnitudes are repurposed for symbolic thinking in humans (Dehaene & Cohen, 2007). Researchers hypothesized that if the ancient systems that evolved to process nonsymbolic numerical magnitudes are indeed repurposed for symbolic thinking, then different number formats (i.e., ‘3’, ‘three’, and ‘•••’) would be processed in the same way (i.e., abstractly). Therefore, researchers have examined whether numerical magnitudes are processed abstractly, using a single format-independent number processing system, or if the underlying representations that support symbolic and nonsymbolic numerical magnitude processing are format-dependent (Ansari, 2016; Cohen Kadosh & Walsh, 2009; Coolidge & Overmann, 2012; Dehaene et al., 1998). Despite years of research, it remains hotly debated whether symbolic numerical thinking is rooted in the evolutionarily ancient system used to process nonsymbolic numerical magnitudes.

1.3 Number Processing is Abstract

For decades, the dominant perspective in the field of numerical cognition has been that symbolic and nonsymbolic numerical quantities are processed using an evolutionarily ancient abstract number processing system that supports numerical magnitude processing, regardless of number format (Brannon, 2006; Dehaene, 2007; Dehaene, Piazza, Pinel, & Cohen, 2003; Halberda, Mazzocco, & Feigenson, 2008; Nieder & Dehaene, 2009). This idea has been supported by findings from both behavioural and neuroimaging research in adult and child populations.

This dominant view, that symbolic and nonsymbolic numbers are processed using the same abstract number processing system, was first supported by the finding that similar behavioural effects are obtained for symbolic and nonsymbolic numerical stimuli when participants make comparative judgements between two numerical magnitudes (Dehaene et al., 1998; Fias, Lammertyn, Reynvoet, Dupont, & Orban, 2003; Fulbright, Manson, Skudlarski, Lacadie, & Gore, 2003; Holloway & Ansari, 2009; Holloway & Ansari, 2008; Moyer & Landauer, 1967). Two examples of behavioural effects that have been reported during both symbolic and nonsymbolic numerical magnitude comparison tasks are the *distance effect* and the *size effect*. The distance effect refers to the finding that participants are faster and more accurate when comparing numbers – be they symbolic or nonsymbolic – if the distance between the two numbers being compared is relatively large (Buckley & Gillman, 1974; Krajcsi, 2017; Moyer & Landauer, 1967). For example, participants are typically faster and more accurate when comparing the numerical magnitudes ‘2’ and ‘8’ (a distance of 6) compared to ‘2’ and ‘3’ (a distance of 1). Complementary, the size effect is the finding that participants are faster and more accurate at comparing numerical magnitudes, again both symbolic and nonsymbolic, when the magnitudes are smaller (e.g., 1 vs. 2) compared to larger magnitudes (e.g., 8 vs. 9), when holding distance constant (Krajcsi, 2017; Moyer & Landauer, 1967). Distance and size effects (i.e., the effects that number comparisons are easier with large distances or small sizes) often combined into a single effect thought to reflect both distance and size, referred to as the *ratio effect* (Krajcsi, 2017). Distance, size and ratio effects have often interpreted to be a measure of representational precision (Nieder & Dehaene, 2009;

Verguts & Fias, 2004). These reports of similar behavioural signatures for the processing of symbolic and nonsymbolic numerical magnitudes that have been replicated across many studies (Buckley & Gillman, 1974; Holloway & Ansari, 2008; Holloway, Price, & Ansari, 2010; Krajcsi, Lengyel, & Kojouharova, 2016; Moyer & Landauer, 1967), including developmental samples (e.g., Holloway & Ansari, 2008, 2009), have ultimately been taken as evidence of shared underlying representations (Dehaene, 2007; Dehaene et al., 1998).

In addition to behavioural data in both adults and children suggesting that symbolic and nonsymbolic numerical magnitudes produce similar behavioural effects, researchers have canvassed the human brain, using neuroimaging methodologies, in search of brain regions that support both symbolic and nonsymbolic numerical magnitude processing (For review see: Sokolowski & Ansari, 2016). Many neuroimaging studies have reported overlapping neural activation during symbolic and nonsymbolic numerical magnitude processing in adults (e.g., Holloway, Price, & Ansari, 2010; Piazza, Pinel, Le Bihan, & Dehaene, 2007; Pinel, Piazza, Le Bihan, & Dehaene, 2004) as well as children (e.g., Cantlon, Libertus, et al., 2009; Holloway & Ansari, 2010). Regions of overlap are typically found along the bilateral intraparietal sulcus (hIPS). In view of this, the hIPS has been identified as an abstract number processing region (Cantlon, Brannon, Carter, & Pelphrey, 2006; Dehaene, 2007; Dehaene et al., 2003; Fias et al., 2003; Piazza et al., 2007; Santens, Roggeman, Fias, & Verguts, 2010). Researchers have taken the finding that the same brain regions support different formats of numerical magnitudes to suggest that symbolic numerical magnitudes are processed using the ancient system that evolved to process nonsymbolic numerical magnitudes. In other words, the evolutionarily ancient system used to process nonsymbolic numerical magnitudes has been repurposed to be an abstract number processing system that is used to process numerical magnitudes of all formats. Together, these behavioural and neuroimaging findings in adults and children have led researchers to conclude that symbolic and nonsymbolic numerical magnitudes are represented using the same abstract number processing system.

1.4 Number Processing is Format-Dependent

Although many have argued, against the background of evidence reviewed above, that symbolic and nonsymbolic numerical magnitudes have the same underlying representations, recent evidence has suggested otherwise. Indeed, a growing body of data has accumulated that suggests that symbolic and nonsymbolic numerical magnitude processing is more distinct than previously assumed (Ansari, 2007; Bulthé, De Smedt, & Op de Beeck, 2014; Cohen Kadosh & Walsh, 2009; Lyons, Ansari, & Beilock, 2012, 2014; Lyons & Beilock, 2013; Sokolowski & Ansari, 2016). Here, I outline several important behavioural and neuroimaging findings that support this claim.

A key study that supports the idea that symbolic and nonsymbolic numerical magnitudes are supported by distinct systems, examined participant's performance on a number comparison task when the two stimuli being compared were either the same format (i.e., both symbolic or both nonsymbolic) or different formats (i.e., comparing a symbolic numerical magnitude to a nonsymbolic numerical magnitude) (Lyons et al., 2012). Critically, if symbolic and nonsymbolic numerical magnitudes are indeed supported by an abstract number processing system, one would predict that there would be no cost of mixing. In other words, conditions during which participants compared symbolic numerical magnitudes to nonsymbolic numerical magnitudes should not differ significantly from conditions where participants compared numerical magnitudes within the same format. However, results revealed that when participants directly compared a symbolic numerical magnitude to a nonsymbolic numerical magnitude they were slower and less accurate than when they compared two numerical magnitudes that were the same format (i.e., two symbolic numerical magnitudes or two nonsymbolic numerical magnitudes) (Lyons et al., 2012). This suggests that the way that humans process symbolic and nonsymbolic numerical magnitudes may be more distinct than has been assumed. Converging recent behavioural evidence has revealed that the similar behavioural effects (namely the distance, size, and ratio effects) observed during comparison tasks for symbolic and nonsymbolic numerical magnitudes do not correlate with each other, and may, in fact, be produced by two distinct systems (Krajcsi, 2017; Krajcsi et al., 2016). Notably, the finding that ratio effects (i.e., the single effect thought to encompass both distance and size effects) for symbolic and nonsymbolic numerical magnitude processing are not as related to each other as has been assumed has also been reported in a cross-sectional developmental sample (Lyons, Nuerk, & Ansari, 2015). Specifically, in a longitudinal sample of almost 2000 children, researchers revealed that the whether a child's nonsymbolic ratio effect was significant was not predictive whether the same was true of that child's symbolic ratio effect. In other words, the presence of a nonsymbolic ratio effect is not related to the presence of a symbolic ratio effect at the individual level. These findings converge with data from human adults (e.g., Krajcsi, 2017; Krajcsi et al., 2016; Lyons et al., 2012) to suggest that perhaps symbolic and nonsymbolic numerical magnitudes are supported by distinct, systems that have some similarities that lead to similar behavioural signatures. Krajsci and colleagues hypothesize that while nonsymbolic numerical magnitudes are likely represented using an evolutionarily ancient approximate magnitude system, symbolic numerical magnitudes may be supported by a discrete semantic system. Here, the term 'discrete' refers to a set of items where each item is distinct (i.e., the quantity of an array of dots). This is in contrast to the term continuous, which refers to a set that can take on any value within a finite or infinite interval (e.g., the amount of physical space taken up by an array of dots). In a discrete semantic system, representations of symbolic numerical magnitudes are stored as values in a semantic network, that operates similarly to a mental lexicon or a conceptual network (Krajcsi, 2017; Krajcsi et al., 2016). Together, these findings contribute to a growing body of behavioural research that suggests that symbols and quantities are not processed as similarly as had previously been concluded.

In addition to the behavioural evidence, discussed above, neuroimaging studies have revealed distinct neural activity supporting the processing of symbolic and nonsymbolic magnitudes using both traditional univariate analysis techniques as well as newer cutting-edge multivariate approaches (Ansari, 2007; Bulthé et al., 2014; Cohen Kadosh et al., 2011; Fias et al., 2003; Holloway et al., 2010; Lyons et al., 2014; Lyons & Beilock, 2018; Santens et al., 2010). In traditional univariate analyses, a General Linear Model (GLM) is used to fit a model to the time course of each voxel independently within a region of interest or at the whole-brain level. Notably, a voxel is a 3D pixel within the brain. Univariate analyses provide insight into whether a set of voxels in a particular area of the brain are significantly activated in relation to a particular stimulus. When using a multivariate analytic approach, the patterns of activation that would normally be averaged are analyzed and compared between conditions. More specifically, using multivariate analytic techniques allows for the examination and comparison of distributed patterns of activity within a region of interest or at the whole-brain level. Indeed, studies that include univariate analyses (i.e., analyses where each voxel is examined independently) reveal spatially distinct patterns of activation for symbolic compared to nonsymbolic numerical magnitudes (e.g., Bulthé et al., 2014; Lyons & Beilock, 2013). Relatedly, studies that used multivariate analyses (i.e., analyses that explore patterns of activation within regions) indicate that the patterns of brain activation differ greatly between symbolic and nonsymbolic numerical magnitude processing both within the hIPS and at the whole-brain level (e.g., Bulthé, De Smedt, & Op de Beeck, 2014; Lyons et al., 2015). Taken together, these neuroimaging data indicate that there are many brain regions along the frontal and parietal lobes that represent numerical magnitude processing in a format-dependent way (For review see: Sokolowski & Ansari, 2016). Moreover, even the regions that exhibit spatial overlap at the univariate level typically have distinct patterns of activation at the multivariate level. This more recent body of evidence highlights that the extent to which symbolic and nonsymbolic numerical magnitudes are processed using common representations should be more carefully examined. Additional research is needed to unravel whether the similarities between symbolic and nonsymbolic numerical magnitude processing are due to the fact that these distinct formats of numerical magnitudes are processed using a shared abstract number processing system, or if instead symbolic and nonsymbolic numerical magnitudes are processed using two distinct systems that have some similarities.

1.5 The Role of Non-Numerical Magnitudes

To complicate matters further, the processing of non-numerical magnitudes (such as physical size, duration, and luminance) have been reported to exhibit similar effects to the processing of symbolic and nonsymbolic numerical magnitudes, both at the behavioural and the neural level (Cantlon, Platt, & Brannon, 2009; Cohen Kadosh, Lammertyn, & Izard, 2008; Sokolowski, Fias, Bosah Ononye, & Ansari, 2017).

In addition to the similarities between symbolic, nonsymbolic and non-numerical magnitude processing, research has shown that the stimuli that are commonly used to assess nonsymbolic numerical magnitude processing are inherently confounded by non-numerical magnitudes such as the size of the dots, and density of the dots (For review see: Leibovich & Henik, 2013). For example, if there are four dots in one array and three dots in another array and all the dots are of the same size, the four dots have a greater total surface area than the three dots. To control for surface area, the size of the dots can be adjusted to equate the total surface area. However, doing this changes the density and the average size of the dots. Therefore, when judging which of three or four dots is greater, participants can use either nonsymbolic numerical magnitude, a non-numerical magnitude (such as surface area), or a combination thereof. Researchers have interpreted this data to suggest that the processing of numerical quantities is sub-served by a general magnitude system, rather than a system (or systems) that are specific to discrete numerical stimuli (Henik, Leibovich, Naparstek, Diesendruck, & Rubinsten, 2011; Sokolowski, Fias, Bosah Ononye, et al., 2017). Therefore, in addition to a lack of conclusive evidence regarding whether symbolic and nonsymbolic numerical magnitudes are sub-served by a single abstract number processing system or distinct format-dependent systems, it is also of great importance to examine how numerical the processing of nonsymbolic stimuli (e.g., arrays of dots) actually is, and consequently examine the extent to which the processing of non-numerical variables plays a central role in nonsymbolic numerical magnitude processing.

1.6 The Acquisition of Symbolic Number Knowledge

The data reviewed above suggest that representing numerical magnitudes symbolically involves processes that are at distinct from the way that nonsymbolic numerical magnitudes are processed in human adults. These conclusions contradict the dominant perspective in the field of numerical cognition: that symbolic and nonsymbolic numerical magnitudes are processed using a single abstract number processing system. From a developmental perspective, the dominant assumption in the field of numerical cognition would support the idea that symbolic representations are formed by mapping arbitrary labels onto pre-existing representations of nonsymbolic numerical magnitudes (Cantlon, 2012; Dehaene, 2007; Nieder & Dehaene, 2009; Piazza, 2010). However, a plausible alternative mechanism is that symbolic and nonsymbolic numerical magnitude processing are supported with similar but distinct mechanisms (Ansari, 2008; Leibovich & Ansari, 2016). A key question that follows is: what would be the best developmental approach to investigating the relationship between symbolic and nonsymbolic numerical magnitude processing across developmental time?

The majority of the research that has measured symbolic and nonsymbolic numerical magnitude processing across developmental time has compared symbolic and nonsymbolic numerical magnitude processing within a sample of older child participants who have already acquired comprehensive knowledge of the symbolic number system (e.g., Bartelet, Vaessen, Blomert, & Ansari, 2014; Holloway & Ansari, 2009; Holloway & Ansari, 2008; Lyons & Ansari, 2015; Lyons et al., 2015; Reynvoet & Sasanguie, 2016; Sasanguie, Defever, Maertens, & Reynvoet, 2013). As with the adult data, this data seems to suggest that symbolic and nonsymbolic numerical magnitudes are not as linked as has been previously assumed and may, in fact, be supported by distinct mechanisms. However, a key developmental approach for investigating the relation between symbolic and nonsymbolic representations of numerical magnitudes is to probe at the link between symbolic and nonsymbolic numerical magnitude processing during the developmental window where children are in the process of acquiring symbolic number knowledge (Batchelor, Keeble, & Gilmore, 2015; Dehaene, 2007; Gunderson et al., 2015; Le Corre & Carey, 2007; Mix, 1999, 2008; Mussolin, Nys, Leybaert, & Content, 2014; Negen & Sarnecka, 2015; Shusterman et al., 2016, 2017; Slusser & Sarnecka, 2011; Slusser, Ditta, & Sarnecka, 2013; Wagner & Johnson, 2011). Before I describe the findings from research examining the link between learning the meaning of symbolic numerical magnitudes and nonsymbolic numerical magnitude processing I will briefly outline the developmental process of acquiring symbolic number knowledge.

Learning the meaning of symbolic numerical magnitudes is a slow process that typically takes children several years to master. Children acquire the ability to recite the count sequence, procedurally, before understanding the semantic meaning of number words and Arabic digits (Karen Wynn, 1990, 1992). Typically, it takes children two to three years from the time they master the count sequence to master the *principle of cardinality* (often referred to as the cardinal principle (CP)): that the last number word that is stated when counting a set refers to the total quantity of objects within that set (Gelman & Gallistel, 1978). The gradual process of acquiring the cardinal principle (i.e., becoming a cardinal principle knower) is as follows. First, children do not know the cardinal meaning of any number words and are consequently referred to as “pre-knowers.” Following this, children learn the meaning of small number words (i.e., numbers one to four) in a step-wise manner (Wynn, 1992). Children who know the meaning of the word ‘one’ and are referred to as “one-knowers.” Several months later, children learn the meaning of the word ‘two’ and therefore have progressed to being “two-knowers”. Subsequently, over time children become “three-knowers,” and some studies report the presence of “four-knowers.” This set of children who know the meaning of some small verbal number words (i.e., words one to four), but have not yet mastered the principle of cardinality (i.e., they do not understand that all number words in their count sequence refer to specific numerical magnitudes and that the last number counted refers to the total quantity of items in a set) are collectively referred to as “subset-knowers.’ Children who have learned the cardinal principle (i.e., CP-knowers) are qualitatively different from subset-knowers in that they can generate cardinality for all numbers using their knowledge of the cardinal principle (Le Corre & Carey, 2007). It is only once children have learned the cardinal principle that they are considered to have a preliminary understanding of the meaning of symbolic numerical magnitudes.

Research exploring the link between learning the semantic meaning of symbolic numerical magnitudes and the ability to process nonsymbolic numerical magnitudes has resulted in mixed findings (e.g., Batchelor, Keeble, & Gilmore, 2015; Dehaene, 2007; Gunderson et al., 2015; Le Corre & Carey, 2007; Mix, 1999, 2008; Mussolin, Nys, Leybaert, & Content, 2014; Negen & Sarnecka, 2015; Shusterman et al., 2016, 2017; Slusser & Sarnecka, 2011; Slusser, Ditta, & Sarnecka, 2013; Wagner & Johnson, 2011). Indeed, some research indicates there is a link between children’s symbolic number knowledge and their ability to discriminate between nonsymbolic numerical magnitudes (e.g., Wagner & Johnson, 2011) whereas other research has indicated that children’s ability to process nonsymbolic numerical magnitudes is independent of that child’s developing understanding of the meaning of symbolic numbers (Le Corre & Carey, 2007; Negen & Sarnecka, 2015).

This body of research that has examined the link between symbolic and nonsymbolic numerical magnitudes during the developmental window where children are acquiring symbolic number knowledge (i.e., learning verbal number words) does not entirely support the assumption, based on the dominant perspective in the field of numerical cognition, that symbols are learned by mapping arbitrary labels onto a pre-existing evolutionarily ancient system used to processing nonsymbolic numerical magnitudes (Dehaene, 2007, 2008; Shusterman et al., 2016; Wagner & Johnson, 2011). More specifically, findings that suggest that preschool-age children's nonsymbolic numerical magnitude processing abilities correlate with early symbolic number abilities (e.g., Mussolin et al., 2014; Wagner & Johnson, 2011) have been taken as support for the idea that children learn abstract number symbols by attaching the arbitrary number symbol onto a pre-existing nonsymbolic numerical magnitude representation. However, there is a growing body of evidence that contradicts this dominant assumption (For a comprehensive review see: Leibovich & Ansari, 2016; Merkley & Ansari, 2016). For example, research has reported that some children can count out an exact number of objects when asked to do so but did not use the corresponding number words when asked to map verbal number words onto nonsymbolic numerical magnitudes (Le Corre & Carey, 2007). Relatedly, when the nonsymbolic numerical magnitude processing task is modified to make sure that children respond on the basis of numerical magnitude (rather than correlated non-numerical magnitude cues), the correlation between verbal number knowledge and nonsymbolic numerical magnitude processing abilities in typically developing children disappears (Negen & Sarnecka, 2015). These data suggest that the link between symbolic and nonsymbolic numerical magnitude processing is not as straightforward as previously assumed. Consequently, these data have driven researchers to question whether there is indeed a causal, developmental relationship between nonsymbolic numerical magnitude processing and the acquisition of the capacity to conceptualize numbers symbolically (Barner, 2017; Merkley & Ansari, 2016).

An alternative explanation that may explain the link between nonsymbolic number processing and the acquisition of the cardinal principle in young children is that learning the cardinality of symbols may facilitate and even constrain children's understanding of discrete nonsymbolic numerical magnitudes. This idea is supported by evidence showing that children's verbal number knowledge was a stronger predictor of nonsymbolic numerical magnitude processing seven months later than the reverse relationship between nonsymbolic numerical magnitude processing acuity and subsequent verbal number knowledge (Mussolin, Nys, Leybaert, et al., 2014). This finding, in conjunction with other data suggesting that CP-knowers outperform subset knowers on a variety of nonsymbolic numerical magnitude tasks (e.g., Batchelor, Keeble, & Gilmore, 2015; Mix, Sandhofer, Moore, & Russell, 2012; Slusser & Sarnecka, 2011; Slusser, Ditta, & Sarnecka, 2013), suggests that the relationship between symbolic and nonsymbolic numerical magnitude processing in children who are in the process of learning symbolic numbers may be bidirectional, rather than unidirectional (Goffin & Ansari, 2019). More research is needed to unravel whether acquiring the ability to represent numbers symbolically influences how children conceptualize discrete nonsymbolic numerical magnitudes.

1.7 Summary and Outstanding Questions

The field of numerical cognition has been dominated by the question of how numerical symbols are connected to evolutionarily ancient, pre-existing, representations of nonsymbolic numerical magnitudes (Dehaene, 2007). However, despite decades of research, it remains fiercely contested whether the uniquely human capacity to process numerical magnitudes symbolically is underpinned by mechanisms that are overlapping or distinct from the evolutionarily ancient system used to process nonsymbolic numerical magnitudes (for review see: (Ansari, 2008; Cohen Kadosh & Walsh, 2009; Sokolowski & Ansari, 2016). Moreover, additional research is needed to understand how the system(s) that support symbolic and nonsymbolic numerical magnitudes emerge over the course of development (for review see: Leibovich & Ansari, 2016; Merkley & Ansari, 2016).

One potential explanation for these contradictory findings is that the relation between symbolic and nonsymbolic numerical magnitude processing may not be static. Indeed, perhaps numbers can be processed both abstractly and in a format-dependent way depending on the cognitive demands of the task and the individual's developmental stage. Testing this idea requires an examination of whether the association between symbolic and nonsymbolic numerical magnitude processing changes when cognitive demands of the task change. For example, one could examine whether the processing of symbolic and nonsymbolic numerical magnitudes differ depending on whether the task requires participants to estimate, manipulate or ignore the magnitude of the stimuli.

The key goal of the current thesis is to explore the link between symbolic and nonsymbolic numerical magnitude processing, both behaviourally and at the neural level, as well as examine how this relationship can be influenced by task factors. Specifically, in adults, I explore the relationship between symbolic and nonsymbolic numerical magnitude processing in the brain by extracting regularities across a large set of studies with various task tasks demands; and by examining processing of symbolic and nonsymbolic numerical magnitude processing in the absence of task demands; and manipulating task conditions intended to make the numerical magnitude more or less salient. In children, I explore the link between the acquisition of symbolic number knowledge and spontaneously attending to nonsymbolic numerical magnitudes. Together, these different approaches provide novel insights into the way humans process symbolic and nonsymbolic numerical magnitudes, both behaviourally and at the neural level, under different attentional conditions and at different points in development.

1.8 Overview of the Current Thesis

Many researchers have canvassed the brain in search of brain systems that support symbolic and nonsymbolic numerical magnitude processing. Although researchers have probed at this question using cutting-edge neuroimaging techniques for nearly two decades, there is a lack of convergence among these neuroimaging studies regarding which brain regions support symbolic and nonsymbolic numerical magnitude processing. Consequently, it remains unclear whether the human brain represents numerical magnitudes abstractly, or if representations of numerical magnitudes in the human brain are format-dependent. In chapter 2 of this thesis, I quantitatively evaluate available neuroimaging evidence to examine whether symbolic and nonsymbolic numerical magnitudes are supported by common or distinct brain regions at the meta-analytic level. Specifically, I use activation likelihood estimation (ALE) to conduct the first quantitative meta-analysis of 57 empirical neuroimaging papers examining neural activation during symbolic and nonsymbolic numerical magnitude processing. This method is a necessary first step to quantify previous research that has examined symbolic and nonsymbolic numerical magnitude processing in order to identify whether the adult human brain hosts abstract and/or format-dependent representations of numerical magnitudes. This study has been published journal *Neuroimage* (Sokolowski, Fias, Mousa, & Ansari, 2017).

As revealed in chapter 2, a large body of research has examined the neural correlates of symbolic and nonsymbolic numerical magnitude processing (Sokolowski, Fias, Mousa, et al., 2017). Critically, the majority of these studies use active tasks, and do not adequately control for non-numerical magnitudes that are inherently correlated with nonsymbolic numerical stimuli. In active tasks, it is notoriously difficult to discern whether neural activation is associated with processing the magnitude of the stimulus or with decision making, motor processing, and task difficulty (Göbel, Johansen-Berg, Behrens, & Rushworth, 2004). To overcome the major limitations of active tasks, a small subset of research has used functional Magnetic Resonance Imaging adaptation (fMR-A) paradigms. fMR-A is a passive design that measures the neural correlates associated with a stimulus of interest without requiring participants to make a decision or motor response. This task relies on the principle that neural populations habituate (i.e., adapt) their activity following repeated presentations of the same stimulus (Grill-Spector, Henson, & Martin, 2006). In fMR-A paradigms, a particular stimulus (i.e., the habituation stimulus) is repeatedly presented to evoke adaptation of brain regions associated with encoding this stimulus. Following this period of adaptation, a stimulus that differs in some way from the habituation stimulus (i.e., a deviant stimulus) is presented. The presentation of the deviant stimulus results in a rebound of activation in regions that are associated with the attributes of the particular deviant compared to the habituation stimulus. This rebound of activation in response to a deviant stimulus is referred to as the ‘neural rebound effect’. The extent of the neural rebound effect in response to a deviant is a function of the difference between the adapted stimulus and the deviant.

Despite the large body of research that has examined symbolic and nonsymbolic numerical magnitude processing, no single study has examined the neural underpinnings of both symbolic and nonsymbolic numerical magnitude processing within-subjects, while accounting for the confounds of general magnitude processing (e.g., physical size) and decision making. In chapter 3 of this thesis, I develop and use a method I refer to as *parallel fMR-A*, to investigate which brain regions specifically support the processing of symbolic numerical magnitudes (symbol), nonsymbolic numerical magnitudes (quantity), and physical size (size). In the parallel adaptation task, participants are repeatedly presented with a specific quantity of the same symbol in a white font of a specific size. Following this, one aspect of the stimulus is changed (symbol, quantity, or size) while the other aspects remain constant. Using this design, I examine whether symbolic and nonsymbolic numerical magnitudes as well as non-numerical magnitudes are sub-served by similar or distinct systems in the human adult brain.

In chapter 2 and 3, I explore the way that the human brain represents symbolic and nonsymbolic numerical magnitudes by extracting regularities across a large set of attentional task demands (chapter 2) and by using a paradigm that removes confounds associated with active task demands (chapter 3). Critically, although these two methodologies are useful for developing our understanding of the way the human brain represents symbolic and nonsymbolic numerical magnitudes in the absence of a task, they do not identify the attentional conditions under which symbolic and nonsymbolic numerical magnitudes are either linked or separate. Chapter 4 of this thesis addresses the question of whether the similarities and differences between symbolic and nonsymbolic numerical magnitude processing depend on whether the magnitudes are being processed effortfully or automatically/unintentionally. Specifically, in chapter 4 I develop and implement a *Symbolic-Nonsymbolic Stroop Task* that assesses the effortful and automatic processing of symbolic and nonsymbolic numerical magnitudes. In the Symbolic-Nonsymbolic Stroop task, participants are presented with two adjacent arrays of digits (e.g., 333 vs. 4444) and asked to either indicate the side containing the greater quantity of symbols (i.e., the nonsymbolic task) or the side containing the symbol associated with the greater numerical magnitude (i.e., the symbolic tasks). The task includes congruent trials, where the larger symbolic and nonsymbolic numerical magnitude appeared on the same side of the screen (e.g., 22 vs. 66666), incongruent trials, where the larger symbolic and nonsymbolic numerical magnitude appeared on opposite sides of the screen (e.g., 222222 vs. 66), and neutral trials, where the irrelevant dimension was the same across both sides of the screen (e.g., 22 vs. 66 for nonsymbolic; 22 vs. 222222 for symbolic). Additionally, the numerical distance between the numerical quantities being compared is systematically varied across trials as a way of manipulating the salience of the numerical magnitudes. This manipulation is based on the finding that numerical information is more likely to be processed (i.e., more salient) when the numerical distance between the stimuli being compared is relatively large. Examining whether numerical distance interacts with the effortful and automatic processing of symbols compared to quantities provides additional insight into the structure of the underlying representations supporting symbolic compared to nonsymbolic numerical magnitude processing. Using this task, I examine the effortful and automatic processing of symbolic and nonsymbolic numerical magnitudes to assess if there is an asymmetry in the way that adults attend to these different formats of numerical magnitudes. Identifying 1) whether there is an asymmetry in the way that human adults process symbolic and nonsymbolic numerical magnitudes and 2) if this asymmetry exists during effortful and/or automatic processing of the numerical magnitudes is essential to gain insight into the representational structure of the underlying mechanisms that support symbolic and nonsymbolic numerical magnitude processing.

The findings from chapters 2, 3 and 4 assess whether there is an asymmetry in the way that human adults represent and process symbolic compared to nonsymbolic numerical magnitudes. To understand the origin of the asymmetry between symbolic and nonsymbolic numerical magnitude processing in adults it is critical to examine the relation between these different formats of numerical magnitudes while these systems are developing.

As discussed above, learning the meaning of verbal number words is a major milestone for young children's numerical thinking. Although a large body of research has examined how number words are mapped onto representations of nonsymbolic numerical magnitudes (e.g., Le Corre & Carey, 2007; Wagner & Johnson, 2011), no study to date has examined how the acquisition of verbal number words relates to the degree to which children spontaneously attend to nonsymbolic numerical magnitudes in the world. In Chapter 5 of this thesis, I develop and use *The Train Task* to examine the degree to which preschool-aged children attended to discrete numerical magnitudes over and above attending to physical size. The train task is an un-cued matching task that measures whether children use a number strategy or physical size strategy when being asked to make a train that is the same as the experimenter's train. The study in Chapter 5 identifies whether verbal number word knowledge relates to the degree to which preschool-aged children attend to discrete numerical magnitudes of varied quantities. This final empirical chapter is essential to unravel how learning the association between symbolic and nonsymbolic numerical magnitudes effects how children spontaneously attend to numerical information in their environment.

In summary, the four empirical chapters that follow will present the data that investigates similarities and differences in the way that the human brain processes symbolic and nonsymbolic numerical magnitude, under different attentional conditions. Specifically, the data presented will address the four areas our inquiry described above. Together, they will provide insight into the attentional conditions under which symbolic and nonsymbolic numerical magnitudes are processed similarly and distinctly both behaviorally and at the neural level in adults and young children.

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Chapter 2

2 Common and Distinct Brain Regions in both Parietal and Frontal Cortex Support Symbolic and Nonsymbolic Number Processing in Humans: A Functional Neuroimaging Meta-Analysis

2.1 Introduction

The question of how the human brain represents numbers has been addressed through a multitude of neuroimaging experiments. The overarching results from this rapidly growing body of research are consistent with a large body of neuropsychological evidence (Cipolotti, Butterworth, & Denes, 1991; Dehaene, Piazza, Pinel, & Cohen, 2003). Specifically, neuroimaging research, like preceding neuropsychological studies, has suggested the bilateral parietal lobes, and specifically the bilateral intraparietal sulci, are important brain regions for processing the quantity of a discrete set of items (i.e., number) (for review see: Dehaene et al. 2003; Nieder 2005; Brannon 2006; Ansari 2008).

Humans have the unique ability to represent numbers either symbolically, such as with Arabic symbols (2) or number words (two), or nonsymbolically, appearing as an array of items (••). The system used to process nonsymbolic numbers (e.g.,••), often referred to as the approximate number system, is thought to be innate, meaning that infants are born with the ability to process nonsymbolic numbers (Cantlon, Libertus, et al., 2009) and has a long evolutionary history (Brannon, 2006; Dehaene, Dehaene-Lambertz, & Cohen, 1998). In contrast, the acquisition of the culturally acquired, uniquely human ability to process abstract numerical symbols (e.g., 2 or two) is a product of learning and development and has emerged recently in human evolution (e.g., Ansari 2008; Coolidge and Overmann 2012). Because different stimulus formats can be used to represent the same quantity, numbers are said to have an abstract (i.e., format-independent) quality. As a result, one of the most dominant theories in the cognitive neuroscience of number processing, namely the three parietal circuits model, states that symbolic and nonsymbolic numbers are sub-served by the same underlying neuronal circuitry (Dehaene et al., 1998, 2003). More specifically, the three parietal circuits model (Dehaene et al.,

2003) predicts that three distinct neural systems support different aspects of basic number processing. Importantly, the model was based on a qualitative synthesis of previous literature (Dehaene et al., 2003). This qualitative meta-analysis suggests that the bilateral intraparietal sulci support the processing of abstract numerical magnitudes, the left angular gyrus supports verbal aspects of basic number processing, and the bilateral posterior superior parietal lobules support visual attentional aspects of number processing. To empirically evaluate the parietal circuits model, researchers have canvassed the brain in search of neural responses associated with abstract representations of numbers (e.g., Dehaene et al. 1998, 2003; Brannon 2006; Piazza et al. 2007; Cantlon, Libertus, et al. 2009).

Such efforts have generated a large body of research which has identified bilateral inferior parietal regions as brain regions that respond to numbers across stimulus formats (Dehaene et al., 2003). Specifically, this research revealed that the intraparietal sulcus was activated by numbers when the numerical information was presented symbolically, either as Arabic digits (Ansari, Garcia, Lucas, Hamon, & Dhital, 2005; Chochon, Cohen, van de Moortele, & Dehaene, 1999; Holloway, Price, & Ansari, 2010; Pesenti, Thioux, Seron, & De Volder, 2000), number words (Ansari, Fugelsang, Dhital, & Venkatraman, 2006), or nonsymbolically, such as dot arrays (Ansari & Dhital, 2006; Holloway et al., 2010; Piazza, Izard, Pinel, Le Bihan, & Dehaene, 2004; Piazza et al., 2007; Venkatraman, Ansari, & Chee, 2005). This activation in the intraparietal sulcus during number processing was also found when the stimuli were presented visually (Arabic numerals) or auditorily (Eger, Sterzer, Russ, Giraud, & Kleinschmidt, 2003). Together, these results suggest that the intraparietal sulcus hosts a format and modality independent representation of number. However, the finding that the intraparietal sulcus is consistently activated across varying task types and methodologies do not necessarily imply that number is represented using only an abstract format-independent system.

In recent years, there has been a growing interest in the distinction between the neural correlates of symbolic processing and nonsymbolic processing (Holloway & Ansari, 2010; Lyons, Ansari, & Beilock, 2014; Shuman & Kanwisher, 2004; Venkatraman et al., 2005). Recent empirical research has highlighted striking differences in the brain activation patterns of numerical stimuli based on stimulus format (Ansari, 2007; Cantlon, Libertus, et al., 2009; Holloway et al., 2010; Piazza et al., 2007; Venkatraman et al., 2005). Right-lateralized parietal and frontal regions have been found to show greater activation for nonsymbolic addition compared to symbolic addition (Venkatraman et al., 2005). However, brain regions in the left intraparietal sulcus have been shown to be more finely tuned to numbers presented as Arabic symbols compared to nonsymbolic dot arrays (Piazza et al., 2007). Holloway et al., (2010) directly tested whether the functional neuroanatomy underlying symbolic and nonsymbolic processing is overlapping or distinct. They found overlapping activation for symbolic and nonsymbolic stimuli in the right inferior parietal lobule. They also found that distinct brain regions responded to symbolic compared to nonsymbolic numbers. Specifically, symbolic number processing recruited the left angular gyrus and left superior temporal gyrus while nonsymbolic number processing recruited regions in the right posterior superior parietal lobule (Holloway et al., 2010). These findings imply that distinct brain regions support format-general and format-specific processing of numbers.

This converging evidence that showed that distinct brain regions support format-specific processing led Cohen Kadosh and Walsh, (2009) to mount a significant challenge to the predominant view in the field that number is represented abstractly in the brain. These authors highlighted caveats associated with studies that conclude that number is processed abstractly. For example, Cohen Kadosh and Walsh, (2009) called attention to the fact that many of the conclusions of these studies are based on null results and point out that shared neural representations may be driven by general task-related processing rather than by shared magnitude representations. The authors subsequently proposed the format-dependent processing hypothesis, postulating that the human brain possesses format-specific semantic representations of number.

Although the primary focus in the field of numerical cognition has been on the relationship between activation in the parietal cortex and number processing, converging evidence has shown that brain regions in the bilateral prefrontal and precentral cortex are also consistently activated during numerical processing (Ansari et al., 2005; P Pinel, Dehaene, Rivière, & LeBihan, 2001). The frontal cortex has been identified as important for number processing in single-cell recordings from neurons in non-human primates (Nieder, Freedman, & Miller, 2002; Nieder & Miller, 2004). Additionally, developmental imaging studies have documented that brain activation during numerical processing shifts from the frontal cortex to the parietal cortex across development (Ansari et al., 2005; Cantlon et al., 2006; Kaufmann et al., 2006). A quantitative meta-analysis that synthesized studies examining brain regions that are correlated with basic number processing and calculation tasks in adults further supported the idea that the frontal cortex is important for number processing in adults (Arsalidou & Taylor, 2011). This meta-analysis revealed that large regions of activation in both the parietal and frontal cortex support basic number and calculation tasks. Results showed that calculation tasks elicited greater activation in the prefrontal cortex compared to basic number tasks. Consequently, these authors concluded that the prefrontal cortices are essential in number and computational tasks (Arsalidou & Taylor, 2011). Together, these studies suggest that a frontoparietal network may support the processing of numerical information. Although the large body of research examining numerical processing in adults concluded that the parietal lobes support numerical processing, it remains unclear whether frontal activation is as consistent as parietal activation during numerical processing. One potential explanation that parietal activation is more consistently reported than frontal activation during number processing tasks is that frontal activation may vary more than parietal activation between individuals. Since fMRI methodology cannot measure individual neural firing and requires averaging across many participants (Scott & Wise, 2003), it is possible that frontal activation varies more strongly than parietal activation between individuals. An alternative explanation is that perhaps parietal regions are selected more often than frontal regions in analyses involving regions of interest (ROI). This selection bias could perpetuate an erroneous impression that the parietal lobe is more important than the frontal lobe for processing numbers. Consequently, quantitative meta-analytic tools are needed to overcome this potential unintentional bias within the field of numerical cognition.

While converging evidence supports the notion that the processing of symbolic and nonsymbolic numbers relies on both common and distinct brain regions, this evidence has never been quantitatively synthesized. Previous meta-analyses by Dehaene et al.

(2003), Cohen Kadosh et al. (2008) and Cantlon, Platt, et al. (2009) examining brain activation patterns underlying number processing in adults did not investigate how the brain activation patterns during number processing differ based on number format (i.e., symbolic vs. nonsymbolic). Instead, these qualitative meta-analyses grouped symbolic and nonsymbolic numerical stimuli into a general term: number (See also, Arsalidou & Taylor, 2011; Dehaene et al., 2003; Houdé, Rossi, Lubin, & Joliot, 2010; Kaufmann, Wood, Rubinsten, & Henik, 2011). However, it is critical to examine symbolic and nonsymbolic numerical stimuli separately since a large body of empirical research has highlighted striking differences in the brain activation patterns of symbolic compared to nonsymbolic number processing (Ansari, 2007; Cantlon, Libertus, et al., 2009; Holloway et al., 2010; Piazza et al., 2007; Venkatraman et al., 2005). Additionally, despite converging evidence revealing consistent activation in frontal brain regions (such as the medial frontal gyrus, inferior frontal gyrus and precentral gyrus) during number processing tasks (Ansari et al., 2005; Pinel et al., 2001), previous qualitative analyses focused exclusively on parietal regions (Cantlon, Platt, et al., 2009; Cohen Kadosh et al., 2008; Dehaene et al., 2003). Moreover, these previous meta-analyses used Caret software (Cohen Kadosh et al. 2008; Cantlon, Platt et al. 2009), a tool that is widely used to visualize neuroimaging data by projecting the spatial mappings of brain activation patterns onto a population-averaged brain (Van Essen, 2012; Van Essen et al., 2001). This method of merging foci from several contrasts into a single figure or table has been the most common approach that researchers have used to combine data across studies (Turkeltaub, Eden, Jones, & Zeffiro, 2002). Visualization-based methods like Caret may be safely used for presenting the results of a few studies but should not be used for large sets of studies. The use of this technique requires judgments of convergence or divergence across studies that are largely subjective. This subjectivity is undesirable for rigorous evaluation of the convergence of neuroimaging findings. Therefore, quantitative meta-analytic tools, such as activation likelihood estimation (ALE) are critical for synthesizing studies with varying methodologies and inconsistent findings (Eickhoff et al., 2009; Turkeltaub et al., 2002, 2012).

2.1.1 The Present Meta-analysis

There has been an emergence of quantitative meta-analytic techniques that use coordinate-based approaches to statistically determine concordance across functional imaging studies (Eickhoff et al., 2009; Turkeltaub et al., 2002, 2012). These methods minimize the subjectivity of meta-analyses by using statistical models to determine inter-study trends. The present study uses activation likelihood estimation (ALE) to examine brain activation patterns underlying symbolic and nonsymbolic number processing. The aim of an ALE meta-analysis is to quantify the spatial reproducibility of a set of independent functional magnetic resonance imaging (fMRI) studies. ALE identifies 3D-coordinates (foci) from independent studies and models probability distributions that are centred around foci. The unification of these probability distributions produces statistical whole-brain maps (ALE maps) that show statistically reliable activity across independent studies (Eickhoff, Bzdok, Laird, Kurth, & Fox, 2012; Eickhoff et al., 2009; Laird, Lancaster, & Fox, 2005; Turkeltaub et al., 2002, 2012). The current study is the first study to use ALE to objectively examine brain activity that is overlapping and distinct for symbolic and nonsymbolic numbers. This study aims to reveal which brain regions support abstract and format dependent number processing.

2.2 Materials and Methods

2.2.1 Literature Search and Article Selection

A stepwise procedure was used to identify all relevant research articles. First, the literature was searched using a standard search in the PubMed (http://www.pubmed.gov) and PsychInfo (http://www.apa.org/psychinfo/) databases. Combinations of the key terms “magnitude”, “number*”, “symbol*”, “nonsymbolic”, “PET”, “positron emission”, “fMRI”, “functional magnetic resonance imaging”, “neuroimaging” and “imaging” were entered into these databases. Second, the reference list of all relevant papers found in the first step and all relevant review papers were reviewed. A study was considered for inclusion if it included a passive or active symbolic number task, a passive or active nonsymbolic number task or both symbolic and nonsymbolic number passive or active tasks. The term ‘study’ refers to a paper and the term ‘contrast’ is defined as an individual contrast reported within a paper.

2.2.2 Additional Inclusion/Exclusion Criteria:

1. Studies had to use at least one of the following tasks: comparison, ordering, passive viewing, numerical estimation, numerosity categorization, counting, matching, size congruity, naming or target detection.

    - These studies were chosen to include both explicit and automatic magnitude processing. Studies with tasks that required cognitive processing (such as calculation) were excluded in order to have activation that is specifically related to format-independent or format-dependent magnitude processing.

2. Studies had to include a sample of healthy human adults.

3. Brain imaging had to be done using fMRI or PET.

    - PET and fMRI studies were included because these imaging methods have comparable spatial uncertainty (Eickhoff et al., 2009).

4. Studies had to use whole-brain group analyses with stereotaxic coordinates in Talairach/Tournoux or Montreal Neurological Institute (MNI) space.

    - Contrasts that used only region of interest analyses were excluded.

    - Contrasts that used only multivariate statistical approaches were excluded.

5. Studies had to have a sample size of > 5 participants.

6. Studies had to be written in English.

Fifty-seven studies met the inclusion criteria, providing data on 877 healthy subjects. All of these studies included at least one symbolic and one nonsymbolic number task. See tables 2.1 and 2.2 for a detailed description of the main characteristics of each selected study. Together, these studies reported 575 activation foci obtained from 121 contrasts. The studies were reported in either Talairach or MNI spaces. Studies that reported data in MNI space were transformed into Talairach space using the Lancaster transformation tool (icbm2tal) (Laird et al., 2010; Lancaster et al., 2007).

2.2.3 Analysis Procedure

Quantitative, coordinate-based meta-analyses were conducted using the revised version of the ALE method (Eickhoff et al., 2012, 2009; Turkeltaub et al., 2012). ALE analyses were conducted using GingerALE, a freely available application by Brainmap (http://www.brainmap.org). ALE assesses the overlap between contrast coordinates (i.e., foci) by modelling the coordinates as probability distributions centred on coordinates to create probabilistic maps of activation related to the construct of interest. Specifically, foci reported from contrasts were combined for each voxel to create a modelled activation (MA) map. An ALE null-distribution is created by randomly redistributing the same number of foci as in the experimental analysis throughout the brain. To differentiate meaningful convergence of foci from random clustering (i.e., noise), an ALE algorithm empirically determines whether the clustering of converging areas of activity across contrasts is greater than chance as shown in the ALE null-distribution. In most empirical studies, a single group of subjects perform multiple similar tasks. Therefore, as most studies report many different contrasts, these contrasts use the same participants in the same scanning session. Consequently, the activation patterns produced by different contrasts do not represent independent observations. The ALE algorithm was modified to address this issue (Eickhoff et al., 2009; Turkeltaub et al., 2012). Additionally, an alternative approach of organizing datasets according to subject group (rather than by contrasts) was implemented (Turkeltaub et al., 2012). The current study used the modified ALE algorithm and organizational approach to prevent subject groups with multiple contrasts from influencing the data more than studies in which only a few contrasts are reported from the same group of participants (Turkeltaub et al., 2012).

Two separate ALE maps were created: One for symbolic numbers and one for nonsymbolic numbers. The current study examined brain regions that were active during each of symbolic (both Arabic and verbal) number processing and nonsymbolic number processing. A conjunction ALE analysis was then computed to examine brain regions that were active during both symbolic and nonsymbolic number processing. Contrast analyses were computed between the symbolic number map of activation and the nonsymbolic number map of activation to determine which regions symbolic and nonsymbolic numbers specifically activated.

2.2.4 Single Dataset ALE Maps

Two separate ALE meta-analyses were conducted to examine the convergence of foci for 1) symbolic number processing and 2) nonsymbolic number processing. These two ALE maps used both active and passive contrasts. In addition, three separate ALE meta-analyses were conducted to examine convergent foci for passive number processing: 1) all passive number processing (passive), 2) passive symbolic number processing (passive symbolic), 3) passive nonsymbolic number processing (passive nonsymbolic). All papers were coded using Scribe (either version 2.3 or version 3.0.8). Coordinates were compiled using Sleuth (version 2.4b). ALE meta-analyses were conducted using GingerALE (version 2.3.6). Of the 57 studies, 31 were used to create the symbolic map of activation (477 subjects, 69 contrasts, 265 foci) (cf. Table 2.1) and 26 were used to create the nonsymbolic map of activation (400 subjects, 52 contrasts, 310 foci) (cf. Table 2.2). 13 studies were used to create the passive map of activation (184 subjects, 30 contrasts, 139 foci) (cf. Table 2.3), of which 5 were used to create the passive symbolic map of activation (cf. Table 2.3), and 7 to create the passive nonsymbolic map of activation (cf. Table 2.3). One of the studies only included a conjunction analysis with both symbolic and nonsymbolic stimuli and therefore was not used to create the passive symbolic or passive nonsymbolic map. All ALE analyses were performed in GingerALE using a cluster-level correction that compared significant cluster sizes in the original data to cluster sizes in the ALE maps that were generated from 1000 threshold permutations. This was in order to correct for false-positive clusters that could arise as a result of multiple comparisons within the same voxel. Specifically, these maps had a cluster-level threshold of $p<.05$ and a cluster-forming (uncorrected) threshold of $p<.001$. The ALE maps were transformed into z-scores for display. This recently developed thresholding technique provides a faster, more rigorous analytical solution for producing the null-distribution and addresses the issue of multiple-comparison corrections (Eickhoff et al., 2012). All single dataset ALE maps (symbolic, nonsymbolic and passive) were created using this correction.

Table 2.1 Studies Included in the Symbolic Meta-Analysis

1st Author	Year	Journal	N	Imaging Method	Mean Age	Gender	Task(s)	Contrast Name	Loc
Ansari D	2005	NeuroReport	12	fMRI	19		Comparison	Distance effect (small>large) adults	12
Ansari D	2006	NeuroImage	14	fMRI	21	8F 6M	Size Congruity	Main effect: distance (small > large)	10
								Main effect of distance in the neutral condition (small>large)	7
Ansari D	2007	Journal of Cognitive Neuroscience	13	fMRI	21.5		Comparison	Conjunction of Small and Large symbolic number	8
Attout L	2014	PLoS ONE	26	fMRI	21	15F, 11M	Order Judgment	Distance effect of numerical order	7
Chassy P	2012	Cerebral Cortex	16	fMRI	28	16M	Comparison	Positive Integers<Negative Integers	1

Chen C	2007	NeuroReport	20	fMRI	22.7	10F, 10M	Delayed-number-matching	Unmatched Numbers > Matched Numbers	8
Chochon F	1999	Journal of Cognitive Neuroscience	8	fMRI		4F, 4M	Naming, Comparison	Digit Naming vs. Control	2
								Comparison vs. Control	13
								Comparison vs. Digit Naming	1
Damarla S R	2013	Human Brain Mapping	10	fMRI	25.5	7F, 3M	Passive Viewing	Stable Parietal lobe voxels in Digit-object mode	2
Eger E	2003	Neuron	9	fMRI	27.9	5F, 4M	Target-detection	Modality-related effects: Auditory Numbers >Visual Numbers (fixed-effect)	2
								Modality-related effects: Auditory Numbers >Visual Numbers (random-effect)	4
								Modality-related effects: Auditory Numbers >Visual Numbers	5

								Modality-related effects: Auditory Numbers >Visual Numbers (random-effect)	4
								Numbers > Letters and Colours (fixed-effect)	4
								Numbers > Letters and Colours (random-effect)	2
								Numbers > Letters (fixed-effect)	2
								Numbers > Letters (random-effect)	2
								Numbers > Colours (fixed-effect)	4
								Numbers > Colours (random-effect)	3
Fias W	2003	Journal of Cognitive Neuroscience	18	PET	23	18M	Comparison	Number comparison vs Nonsymbolic Stimuli Comparison	13
Fias W	2007	Journal of Neuroscience	17	fMRI		9F, 8M	Comparison	(Number comparison-number dimming) - (letter comparison-letter dimming)	3

Franklin M S	2009	Journal of Cognitive Neuroscience	17	fMRI	21.8	10F, 7M	Ordering Task	Magnitude Near>Far (common regions with Order Near>Far)	1
								Order Far>Near (common regions with Magnitude Near>Far)	1
								Magnitude Near>Far (Unique regions)	3
								Order Far>Near (Unique regions)	1
Fulbright R K	2003	American Journal of Neuroradiology	19	fMRI	24	8F, 11M	Order, Identification	Number vs Shapes	0
He L	2013	Cerebral Cortex	20	fMRI	21	8F, 12M	Comparison	Symbolic > Nonsymbolic	2
								Digit-digit > cross notation trials	1
								Overlap between (Symbolic>nonsymbolic) and (small>large)	2
Holloway I D	2010	Neuroimage	19	fMRI	23.5	10F, 9M	Comparison	(symbolic - control) - (nonsymbolic - control)	2

Holloway I D	2013	Journal of Cognitive Neuroscience	26	fMRI	25	22F, 4M	Passive Viewing	Adaptation to Hindu-Arabic Numerals for both groups	2
Kadosh R	2005	Neuro-psychologia	15	fMRI	28	7F, 8M	Comparison	Numerical vs. Size	7
								Numerical vs. Luminance	8
								Numerical Distance	3
								Numerical Distance (IPS)	2
Kadosh R C	2007	NeuroImage	17	fMRI	31	7F, 10M	Stroop	Notation Adaptation	2
								Quantity Adaptation	1
								Notation x Adaptation	1
Kadosh R C	2011	Frontiers in Human Neuroscience	19	fMRI	26.3	12F, 7M	Passive Viewing	Magnitude Change Digits	10
								Magnitude Change Digits>Dots	3

Kaufmann L	2005	Neuroimage	17	fMRI	31	7F, 10M	Stroop	Numerical comparison > physical comparison	5
								Numerical comparison (Distance 1 > Distance 4, only neutral trials)	5
Le Clec'H G	2000	Neuroimage	5	fMRI	37	5M	Compare to 12	Numbers > Body Parts (Block)	4
			6	fMRI	27	3F, 3M	Compare to 12	Numbers > Body Parts (Error)	3
Liu X	2006	Journal of Cognitive Neuroscience	23	fMRI		7 F, 5M	Stroop	Distance of 18 vs. Distance of 27	6
Lyons I M	2013	Journal of Cognitive Neuroscience	35	fMRI		16F, 17M	Comparison	Symbolic: Number Ordinal > Luminance Ordinal	3
								Symbolic: Number Ordinal > Luminance Ordinal and Number Cardinal >Luminance Cardinal	10

Notebaert K	2011	Journal of Cognitive Neuroscience	13	fMRI		6F,7M	Passive Viewing	Ratio 1.25 Below > Ratio 1	1
								Ratio 1.5 Below > Ratio 1	1
								Ratio 2 Below > Ratio 1	1
								Ratio 2 Below > Ratio 1.25 Below	1
								Ratio 1.5 Above > Ratio 1	1
								Ratio 2 Above > Ratio 1	1
								Ratio 2 Above > Ratio 1.25 Above	1
Park J	2012	Journal of Cognitive Neuroscience	20	fMRI	23.4	11F, 9M	Visual matching task	Number > Letter	1
Pesenti M	2000	Journal of Cognitive Neuroscience	8	PET		8M	Comparison	Comparison vs. Orientation, Digits	7
Pinel P	1999	NeuroReport	11	fMRI	26	2F, 9M	Compare to 5	Arabic Number > Verbal Number	1

								Close Distance > Far Distance	1
								Far Distance > Close Distance	1
Pinel P	2001	Neuroimage	13	fMRI			Comparison	Verbal vs. Arabic	3
								Arabic vs. Verbal	6
								Distance Effect	7
Pinel P	2004	Neuron	15	fMRI	24	18 F, 6M	Stroop	Number Comparison vs. Size Comparison	5
								Number Comparison Small Distance vs. Number Comparison Large Distance	3
Price G R	2011	Neuroimage	19	fMRI	22.17	6F, 13M	Passive Viewing	(Conjunction) Arabic digits>Letters and Arabic digits>Scrambled digits	1
Vogel S E	2013	Neuro-psychologia	14	fMRI	25	7F, 7M	Number line estimation	Number > Control	10
								Number Specific Activation	5

Loc, number of locations reported in contrast; fMRI, functional magnetic resonance imaging; PET, positron emission tomography; N, sample size of each study; M – Male, F – Female.

Table 2.2 Studies Included in the Nonsymbolic Meta-Analysis

1st Author	Year	Journal	N	Imaging Method	Mean Age	Gender	Task(s)	Contrast Name	Loc
Ansari D	2006	Brain Research	16	fMRI	20.4	16M	Passive Viewing	Number Change Effect	4
Ansari D	2006	Journal of Cognitive Neuroscience	9	fMRI	19.8	6M, 3F	Comparison	Distance Effect in Adults	7
Ansari D	2007	Journal of Cognitive Neuroscience	13	fMRI	21.5		Comparison	Small Nonsymbolic > Large Nonsymbolic	1
								Large Nonsymbolic > Small Nonsymbolic	2
								Conjunction of small nonsymbolic and large nonsymbolic	3
Cantlon J F	2006	PLoS Biology	12	fMRI	25	5F, 7M	Passive viewing	Number > Shape (Adults)	2
Castelli F	2006	PNAS	12	fMRI	24	4F, 8M	Comparison	Estimating Numerosity: In space and time	7
								Difficulty Effect Estimating Numerosity: Space	2

								Difficulty Effect Estimating Numerosity: Time	2
Chassy P	2012	Cerebral Cortex	16	fMRI	28	16M	Comparison	Disk > Dots	1
Damarla S R	2013	Human Brain Mapping	10	fMRI	25.5	7F, 3M	Passive Viewing	Stable Parietal lobe voxels in Pictoral Mode	6
Demeyere N	2014	Human Brain Mapping	12	fMRI	26	9F, 3M	Passive Viewing	Adaptation to categories (repeated pairs vs. different pairs)	4
								Repetition of small category versus large category (large < small)	1
								Repetition of small category versus large category (small < large)	9
								Numerosity specific repetition [Repetition-Category > (Repetition-numerosity + Repetition-Exact)]	14
								Interaction Small/Large with Category/Numerosity/Exact	3
								Small numerosity < Small category	4

Dormal V	2009	Human Brain Mapping	14	fMRI	21	14M	Numerosity Categorization	Numerosity Processing - Reference for Numerosity	9
Dormal V	2012	Human Brain Mapping	15	fMRI	21	15M	Numerosity Categorization	Numerosity - Reference for Numerosity	5
								(Numerosity - Reference for Numerosity) - (Duration vs Reference for Duration)	1
Dormal V	2010	Neuroimage	15	fMRI	21	15M	Numerosity Categorization	[Simultaneous Numerosity]-[Reference Simultaneous Numerosity]	6
								[Sequential Numerosity]-[Reference Sequential Numerosity]	6
								[Simultaneous Numerosity–Reference for Simultaneous Numerosity]-[Sequential Numerosity–Reference Sequential Numerosity]	4
								[Sequential Numerosity-Reference Sequential Numerosity]-[Simultaneous Numerosity-Reference Simultaneous Numerosity]	3

								[Sequential Numerosity]-[Reference Sequential Numerosity] and [Simultaneous Numerosity]-[Reference Simultaneous]	3
Eger E	2009	Current Biology	10	fMRI	23	5F, 5M	Comparison	Number Comparison Same List	8
								Number Comparison Different List	10
Hayashi M J	2013	Journal of Neuroscience	27	fMRI		14F, 12M	Comparison	Main Effect of Numerosity Task	13
He L	2013	Cerebral Cortex	20	fMRI	21	8F, 12M	Comparison	Nonsymbolic > Symbolic	8
								Dot-dot > cross-notation trials	4
								Overlap between (nonsymbolic>symbolic) and (large>small)	6
Holloway I D	2010	Neuroimage	19	fMRI	23.5	10F, 9M	Comparison	(nonsymbolic-control)-(symbolic-control)	7
Holloway I D	2013	Journal of Cognitive Neuroscience	26	fMRI	25	22F, 4M	Passive Viewing	Nonsymbolic Comparison	6

Jacob S N	2009	European Journal of Neuroscience	15	fMRI			Passive Viewing	Dot Proportion full brain analysis	1
								Adaptation to Dot Proportion	27
								Numerosity full brain analysis	1
Kadosh R C	2011	Frontiers in Human Neuroscience	19	fMRI	26.3	12F, 7M	Passive Viewing	Magnitude Change Dots	10
								Magnitude Change Dots>Digits	6
Leroux G	2009	Developmental Science	9	fMRI	23	9M	Number-length interference	(Interference-reference interference) AND (Covariation-Reference covariation)	10
Lyons I M	2013	Journal of Cognitive Neuroscience	33	fMRI		16F, 17M	Comparison	Nonsymbolic: Number ordinal>Luminance Ordinal	7
								Dot Ordinal >Luminance Ordinal (dot) and Dot Cardinal >Luminance Cardinal (dot)	10
Piazza M	2002	Neuroimage	9	PET	29	9M	Count	All 6-9 > All 1-4	8
								6-9 Random > 1-4 Random	6

								6-9 Canonical > 1-4 Canonical	5
Piazza M	2004	Neuron	12	fMRI	23		Passive Viewing	Regions Responding to Deviations in Number	7
Piazza M	2006	Brain Research	10	fMRI		3F, 7M	Estimation, Counting	Estimation > Matching	9
								Counting > Matching	14
								Counting > Estimation	7
Roggeman C	2011	Journal of Neuroscience	23	fMRI	25.8	23M	Passive Viewing	Large vs. Small Numerical Deviants	2
								Far vs. Close Numerical Deviants	1
Santens S	2010	Cerebral Cortex	16	fMRI	22.2	13M, 1F	Match-to-numerosity	conjunction: (Numerosity large > Numerosity medium) and (Numerosity medium > Numerosity small)	6
Shuman M	2004	Neuron	9	fMRI		2F, 7M	Comparison	Experiment 1: Nonsymbolic number comparison > Nonsymbolic colour comparison	2

Loc, number of locations reported in contrast; fMRI, functional magnetic resonance imaging; PET, positron emission tomography; N, Sample size of each study; M – Male, F – Female.

Table 2.3 Studies Included in the Passive Meta-Analyses

1st Author	Year	Journal	N	Imaging Method	Mean Age	Gender	*Symbolic or Nonsymbolic	Contrast Name	Loc
Ansari D	2006	Brain Research	16	fMRI	20.4	16M	Nonsymbolic	Number Change Effect	4
Cantlon J F	2006	PLoS Biology	12	fMRI	25	5F, 7M	Nonsymbolic	Number > Shape (Adults)	2
Damarla S R	2013	Human Brain Mapping	10	fMRI	25.5	7F, 3M	Nonsymbolic	Stable Parietal lobe voxels in Pictoral Mode	6
							Symbolic	Stable Parietal lobe voxels in Digit-object mode	2
Demeyere N	2014	Human Brain Mapping	12	fMRI	26	9F, 3M	Nonsymbolic	Adaptation to categories (repeated categories pairs vs. different categories pairs)	4
								Repetition of small category versus large category (large < small)	1
								Repetition of small category versus large category (small < large)	9

								Numerosity specific repetition [Repetition-Category > (Repetition-numerosity + Repetition-Exact)]	14
								Interaction Small/Large with Category/Numerosity/Exact	3
								Small numerosity < Small category	4
Holloway I D	2013	Journal of Cognitive Neuroscience	26	fMRI	25	22F, 4M	Symbolic	Adaptation to Hindu-Arabic Numerals for both groups	2
Jacob S N	2009	European Journal of Neuroscience	15	fMRI			Nonsymbolic	Line Proportion full brain analysis	1
								Adaptation to Dot Proportion	27
								Numerosity full brain analysis	1
Kadosh R C	2007	NeuroImage	17	fMRI	31	7F, 10M	Symbolic	Notation Adaptation	2
								Quantity Adaptation	1
								Notation x Adaptation	1

Notebaert K	2011	Journal of Cognitive Neuroscience	13	fMRI		6F,7M	Symbolic	Ratio 1.25 Below > Ratio 1	1
								Ratio 1.5 Below > Ratio 1	1
								Ratio 2 Below > Ratio 1	1
								Ratio 2 Below > Ratio 1.25 Below	1
								Ratio 1.5 Above > Ratio 1	1
								Ratio 2 Above > Ratio 1	1
								Ratio 2 Above > Ratio 1.25 Above	1
Piazza M	2004	Neuron	12	fMRI	23		Nonsymbolic	Regions Responding to Deviations in Number	7
Piazza M	2007	Neuron	14	fMRI			**Symbolic & Nonsymbolic	Overall fMRI Adaptation Effect (Activation decrease with repetition of same approximate quantity)	16
								Distance-Dependent Recovery from Adaptation across conditions (Far>Close)	21

Price G R	2011	Neuroimage	19	fMRI	22.17	6F, 13M	Symbolic	(conjunction) Arabic digits>Letters and Arabic digits>Scrambled digits	1
Roggeman C	2011	Journal of Neuroscience	23	fMRI	25.8	23M	Nonsymbolic	Large vs. Small Numerical Deviants	2
								Far vs. Close Numerical Deviants	1

Loc, number of locations reported in contrast; fMRI, functional magnetic resonance imaging; PET, positron emission tomography

*Symbolic vs. Nonsymbolic column shows whether contrast was used in symbolic or nonsymbolic map for format-specific passive viewing maps.

**Study used in the full passive map but not in symbolic or nonsymbolic

2.2.5 Conjunction and Contrast Analyses

Conjunction and contrast analyses were computed to examine overlapping and distinct brain regions for the two ALE maps that included both active and passive tasks for symbolic and nonsymbolic number processing (Eickhoff et al., 2011). All conjunction and contrast ALE analyses were performed in GingerALE and used an uncorrected threshold of p<.01 with 5000 threshold permutations and a minimum volume of 50mm3. Although the cluster-level correction used to produce the single file ALE maps is the optimal thresholding technique available (Eickhoff et al., 2012), this correction is not yet available for conjunction and contrast analysis. The only available correction available to date for conjunction and contrast analysis is false discovery rate (FDR) thresholding. However, because ALE models the foci as 3D Gaussian distributions and FDR is not recommended to be used with Gaussian data (Chumbley & Friston, 2009), an uncorrected threshold of .01 was used for the conjunction and contrast analyses. Therefore, due to methodological constraints, a cluster-level correction was used for the single file maps and uncorrected thresholding for the conjunction and contrast analyses[1,2]. An uncorrected threshold of .01 was appropriate for the conjunction and contrast analyses because the algorithm used by these analyses only includes clusters that have already passed the strict threshold of cluster-level .05 and uncorrected .001, used to create the single file maps. Therefore, this threshold is ideal to ensure that the threshold is stringent

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[1] Leading experts on ALE are recommending against using FDR and thus, for the use of uncorrected thresholds when doing conjunction and contrast analyses.

Discussions on the GingerALE forum:
http://www.brainmap.org/forum/viewtopic.php?f=3&t=499&sid=6c3ba03dfecbce73933a22acbd6fe2c1

http://brainmap.org/forum/viewtopic.php?f=3&t=320#p1012

http://brainmap.org/forum/viewtopic.php?f=3&t=485#p1505

[2] The main findings do not change when using an FDR correction of .05 to calculate the conjunction and contrast analyses comparing symbolic and nonsymbolic single file ALE maps with a cluster-level threshold of p<.05 and a cluster-forming (uncorrected) threshold of p<.05.

without masking any important regions. This threshold was combined with an extent threshold, which suppressed clusters that were smaller than 50 mm^3.

A conjunction analysis was computed to examine the similarity of activation between the ALE maps generated by symbolic number processing and nonsymbolic number processing. The voxel-wise minimum value of the input ALE images was used to create the conjunction map. The conjunction was considered to be significant for each voxel if all contributing ALE maps showed significant activation in that voxel at the thresholds described. A conjunction ALE map was created to determine overlapping activation of symbolic and nonsymbolic numbers.

Contrast analyses were computed to compare activation between the ALE maps generated for symbolic and nonsymbolic number processing. ALE contrast images are created by directly subtracting one input image from the other. GingerALE creates simulated null data to correct for unequal sample sizes by pooling foci and randomly dividing the foci into two groupings that are equal in size to the original data sets. One simulation dataset is subtracted from the other and compared to the true data. This produces voxel-wise p-value images that show where the true data sit in relation to the distribution of values within that voxel. The p-value images are converted to Z scores. The following ALE contrasts were computed: 1) symbolic > nonsymbolic, 2) nonsymbolic > symbolic.

It is possible that the activation commonly found across studies is related to top-down task-related brain activations during the explicit processing of number tasks. Although the majority of neuroimaging studies investigating number processing have used active paradigms in which participants have to make a decision about numerical stimuli being presented, there is a growing body of research that has examined the neural processing of symbolic and nonsymbolic numbers in the absence of an explicit numerical processing task (e.g., Piazza et al. 2004, 2007; Ansari, Dhital, et al. 2006; Holloway et al. 2013; Vogel et al. 2014). In order to determine which brain regions support symbolic and nonsymbolic number processing in the absence of task demands, ALE maps were created included papers which exclusively used passive viewing paradigms. Specifically, an

ALE map was computed to examine convergent activation of all papers that used a passive viewing paradigm (symbolic and nonsymbolic). Additionally, two separate ALE maps were created using papers that employed passive viewing paradigms: One for passive viewing of symbolic numbers and one for passive viewing of nonsymbolic numbers.

There were not enough papers to conduct conjunction and contrast analyses to examine the overlapping and distinct activation for the passive symbolic and passive nonsymbolic single file ALE maps. Therefore, these maps were compared qualitatively.

2.2.6 Anatomical Labeling

Anatomical labels from the Talairach Daemon (talairach.org) were determined automatically using GingerALE software for each of the automatically generated peak ALE locations within all clusters. All (x, y, z) coordinates and anatomical labels of peak ALE values are reported in Table 2.4, Table 2.5 and Table 2.6.

2.3 Results

This section is organized in the following manner. First, the results are presented for the two meta-analyses that include active and passive tasks: 1) symbolic number processing, 2) nonsymbolic number processing. This is followed by the results of the conjunction analysis for symbolic and nonsymbolic magnitude processing. Following this, the brain regions active for the following contrasts are shown for symbolic>nonsymbolic, nonsymbolic>symbolic. These contrast analyses are repeated using a symbolic map that only includes Arabic digits. Subsequently, the results are presented for the three ALE maps that include only passive tasks: 1) passive (both symbolic and nonsymbolic), 2) passive symbolic and 3) passive nonsymbolic. Finally, reliability analyses for the symbolic and nonsymbolic ALE maps are presented.

2.3.1 Single Dataset Meta-Analyses (Passive and Active)

Two separate single dataset ALE meta-analyses were conducted to examine the convergence of foci for symbolic number processing and nonsymbolic number processing.

2.3.1.1 Symbolic ALE Map

The symbolic number processing single dataset meta-analysis revealed activation in a widespread frontoparietal network of brain areas during symbolic number processing (Fig. 2.1 and Table 2.4). The largest clusters of converging brain activation across 31 studies (Table 2.1) were in the left superior parietal lobule, inferior parietal lobule and the precuneus, as well as the right inferior parietal lobule and precuneus. In addition to the parietal lobes, there was convergent activation in the left lingual gyrus and the left middle occipital gyrus as well as in the right superior frontal gyrus.

2.3.1.2 Nonsymbolic ALE map

The nonsymbolic number processing single dataset meta-analysis also revealed activation in a widespread frontoparietal network of brain areas during nonsymbolic number processing (Fig. 2.2 and Table 2.4). Convergent brain activation across 26 studies (Table 2.2) was found in a region spanning the right inferior parietal lobule, superior parietal lobule, precuneus and middle occipital gyrus, as well as a region spanning the left superior parietal lobule and the precuneus. Convergent activation was also found in the, right medial frontal gyrus and cingulate gyrus, the right insula, right precentral gyrus, and left middle occipital gyrus.

Table 2.4 Single Dataset Analyses (Active and Passive)

Hemisphere	Brain Area	BA	X	Y	Z	ALE	Vol/mm
Symbolic							
L	Superior Parietal Lobule	7	-28	-58	42	0.026	8944
L	Superior Parietal Lobule	7	-26	-54	44	0.026	
L	Inferior Parietal Lobule	40	-38	-48	48	0.022	
L	Inferior Parietal Lobule	40	-40	-44	38	0.021	
L	Inferior Parietal Lobule	40	-34	-52	36	0.020	
L	Precuneus	31	-20	-72	30	0.014	
R	Inferior Parietal Lobule	40	34	-44	40	0.031	6208
R	Precuneus	19	30	-64	38	0.028	
R	Precuneus	7	22	-52	46	0.021	
L	Lingual Gyrus	18	-22	-74	-4	0.017	1096
L	Middle Occipital Gyrus	18	-26	-86	2	0.014	
R	Superior Frontal Gyrus	6	2	10	48	0.021	768
Nonsymbolic							
R	Inferior Parietal Lobule	40	44	-40	46	0.032	10448
R	Precuneus	7	28	-50	48	0.030	
R	Superior Parietal Lobule	7	28	-58	46	0.026	
R	Precuneus	7	18	-64	50	0.026	
R	Middle Occipital Gyrus	19	30	-78	18	0.020	
R	Precuneus	31	28	-72	24	0.018	
R	Middle Occipital Gyrus	18	34	-84	4	0.013	
L	Superior Parietal Lobule	7	-30	-54	46	0.032	5472
L	Precuneus	19	-26	-70	30	0.019	
L	Precuneus	7	-22	-64	36	0.018	
L	Precuneus	7	-20	-58	54	0.017	
L	Precuneus	7	-20	-62	44	0.016	
L	Superior Parietal Lobule	7	-26	-52	60	0.012	
R	Medial Frontal Gyrus	32	4	10	46	0.032	3464
L	Cingulate Gyrus	32	-6	12	40	0.013	
R	Insula	13	32	20	8	0.034	1888
R	Precentral Gyrus	6	42	2	28	0.036	1704
L	Middle Occipital Gyrus	19	-26	-88	18	0.020	824

X, Y and Z – x,y,z values of the location of the maximum ALE value

ALE - maximum ALE value observed in the cluster

Vol/mm^3 - volume of cluster in mm$_3$

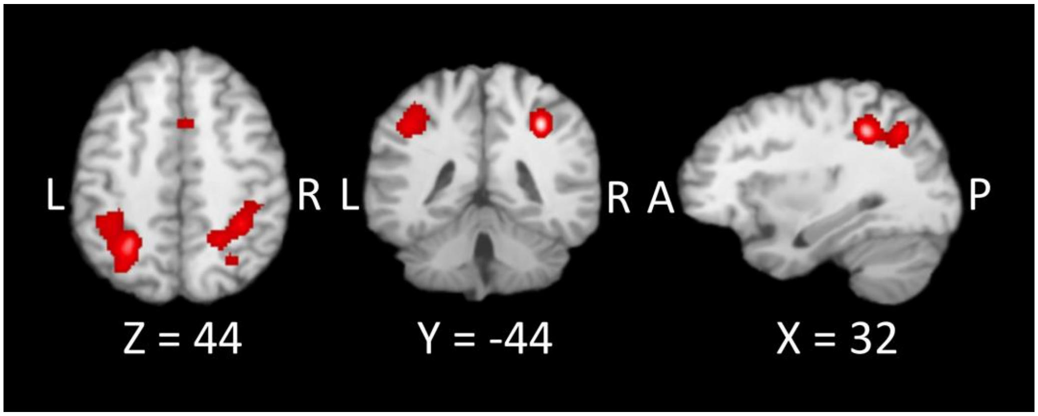

Figure 2.1 Single dataset ALE map of symbolic number processing. The ALE analysis revealed significant clusters of convergent brain clusters (cf., table 2.4). Activations were identified using a cluster-level threshold of p<.05 with 1000 threshold permutations and an uncorrected p<.001 Brain slices are shown at coordinates (x, y, z) in Talairach space.

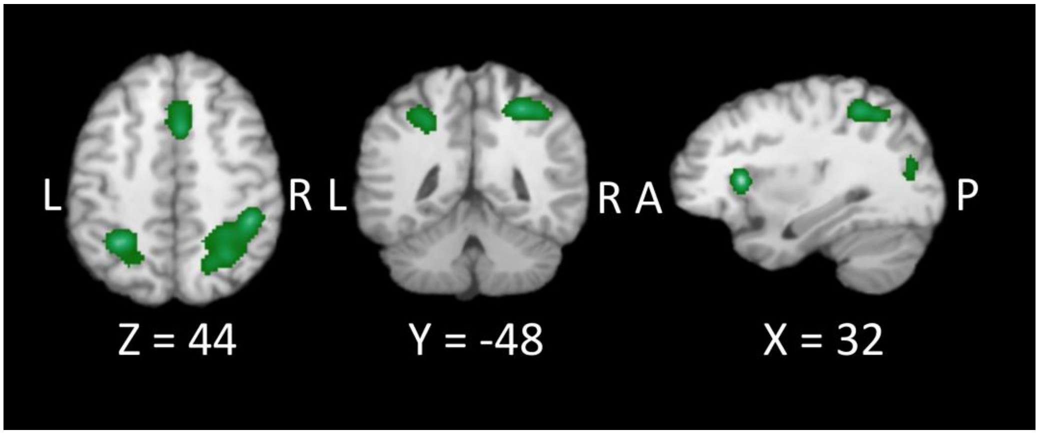

Figure 2.2 Single dataset ALE map of nonsymbolic number processing. The ALE analysis revealed significant clusters of convergent brain clusters (cf., table 2.4). Activations were identified using a cluster-level threshold of p<.05 with 1000 threshold permutations and an uncorrected p<.001 Brain slices are shown at coordinates (x, y, z) in Talairach space.

2.3.2 Conjunction and Contrast Analyses

2.3.2.1 Conjunction ALE Map

A conjunction analysis was conducted to reveal brain regions with convergent clusters of activation between the symbolic and nonsymbolic single dataset ALE maps. Significant clusters of activation for symbolic and nonsymbolic number processing converged in the bilateral inferior parietal lobules, bilateral precuneus, left superior parietal lobule, as well as the right superior frontal gyrus (Table 2.5 Figure 2.3).

2.3.2.2 Contrast ALE Maps

To assess which brain regions were specifically activated for symbolic and nonsymbolic number processing, contrast analyses were conducted to compare the symbolic and nonsymbolic single dataset ALE maps. These contrast analyses revealed significant clusters of activation in the right supramarginal gyrus and inferior parietal lobule, as well as the left angular gyrus, for symbolic>nonsymbolic (Table 2.5, Figure 2.3). There were significant clusters of activation in a right-lateralized frontoparietal network including the superior parietal lobule, inferior parietal lobule, precuneus, insula, superior frontal gyrus, and middle occipital gyrus for nonsymbolic>symbolic (Table 2.5, Figure 2.3).

Table 2.5 Conjunction and Contrast Analyses

Hemisphere	Brain Area	BA	X	Y	Z	ALE	Vol/mm
Symbolic and Nonsymbolic							
L	Superior Parietal Lobule	7	-26	-54	44	0.026	2544
L	Inferior Parietal Lobule	40	-34	-48	44	0.016	
R	Precuneus	7	22	-52	46	0.021	2464
R	Inferior Parietal Lobule	40	36	-46	44	0.020	
R	Inferior Parietal Lobule	40	38	-42	42	0.020	
R	Inferior Parietal Lobule	40	32	-46	44	0.019	
R	Precuneus	19	30	-62	42	0.017	
R	Superior Frontal Gyrus	6	2	10	48	0.021	728
L	Precuneus	7	-28	-66	32	0.014	184
L	Precuneus	7	-26	-64	36	0.013	
L	Precuneus	19	-24	-72	30	0.012	
R	Precuneus	7	22	-66	38	0.012	24
R	Precuneus	7	24	-66	36	0.012	8
Symbolic > Nonsymbolic							
R	Supramarginal Gyrus	40	36	-48	32	2.911	304
R	Inferior Parietal Lobule	40	34	-52	34	2.820	
L	Angular Gyrus	39	-36	-60	36	2.878	240
Nonsymbolic > Symbolic							
R	Precuneus	7	18	-61	51	2.848	1128
R	Precuneus	7	15.5	-64.5	52	2.820	
R	Superior Parietal Lobule	7	21.3	-66.7	51.3	2.794	
R	Insula	13	38	20	11	3.156	648
R	Insula	13	32	20	14	2.636	
R	Inferior Parietal Lobule	7	34	-56	46	3.156	440
R	Inferior Parietal Lobule	40	34	-48	54	2.794	
R	Superior Frontal Gyrus	6	8	22	50	3.156	408
R	Inferior Parietal Lobule	40	46	-44	49	2.652	328
R	Middle Occipital Gyrus	19	34	-80	12	2.687	200

X, Y and Z – x,y,z values of the location of the maximum ALE value

ALE – conjunction analysis: maximum ALE value observed in the cluster, contrast analyses: maximum z-score observed in the cluster

Vol/mm^3 - volume of cluster in mm3.

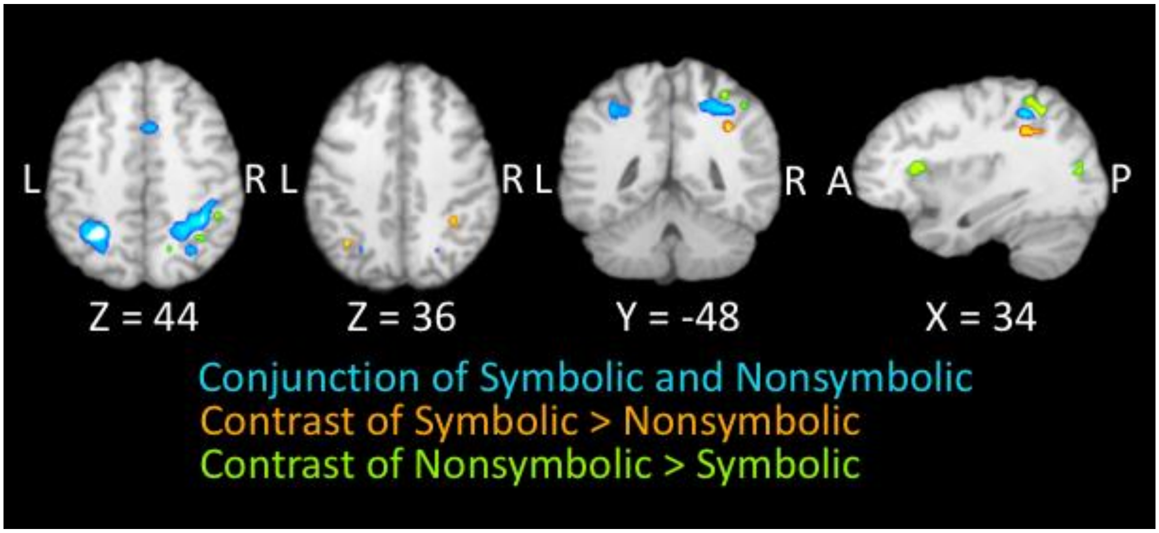

Figure 2.3 ALE maps of the conjunction and contrasts between the symbolic and nonsymbolic single dataset ALE maps. The ALE conjunction analysis revealed significant clusters of convergence between symbolic and nonsymbolic (blue). ALE contrast analyses reveal specific activation for symbolic>nonsymbolic (orange) and nonsymbolic>symbolic (green). Conjunction and contrast analyses were conducted using an uncorrected p<.01 with a minimum volume of 50mm3. Brain slices are shown at coordinates (x, y, z) in Talairach space.

2.3.2.3 Contrast ALE Maps (Arabic Digits Only)

Of the 31 studies, which were included in the symbolic single file ALE map, 24 studies visually presented Arabic digits. Of the remaining 8 studies, 2 visually presented either number words or a combination of number words and Arabic digits, and 6 studies used both visual and auditory presentations of numbers. In order to determine whether the significant clusters of activation revealed by the symbolic vs. nonsymbolic contrast analyses were driven by the diversity of the symbolic number formats, a single dataset ALE map was created containing papers that contrasted Arabic digits (24 papers, 399 subjects, 43 contrasts, 172 foci). To assess which brain regions were specifically activated for Arabic digits and nonsymbolic number processing, contrast analyses were conducted to compare the Arabic digit and nonsymbolic single dataset ALE maps.

These contrast analyses revealed significant clusters of activation in the left inferior parietal lobule and precuneus for Arabic digits>nonsymbolic (Table 2.6, Figure 2.4). There were significant clusters of activation in a right-lateralized frontal-parietal network including the superior parietal lobule, insula, and medial frontal gyrus, nonsymbolic>Arabic digits (Table 2.6, Figure 2.4).

Table 2.6 Contrast Analyses: Arabic Digits vs. Nonsymbolic

Hemisphere	Brain Area	BA	X	Y	Z	ALE	Vol/mm
Arabic Digits > Nonsymbolic							
L	Inferior Parietal Lobule	39	-35	-62	40	2.590	152
L	Precuneus	19	-30	-62	40	2.576	
Nonsymbolic > Arabic Digits							
R	Superior Parietal Lobule	7	23.1	-62.5	53.3	3.719	2064
R	Superior Parietal Lobule	7	38	-57	48	3.540	
R	Inferior Frontal Gyrus	13	38	24	8	2.948	416
R	Insula	13	38	20	12	2.911	
R	Insula	13	36	24	12	2.848	
R	Medial Frontal Gyrus	8	9.3	21.3	48.7	2.794	208

X, Y and Z – x,y,z values of the location of the maximum ALE value

ALE – conjunction analysis: maximum ALE value observed in the cluster, contrast analyses: maximum z-score observed in the cluster

Vol/mm^3 - volume of cluster in mm^3

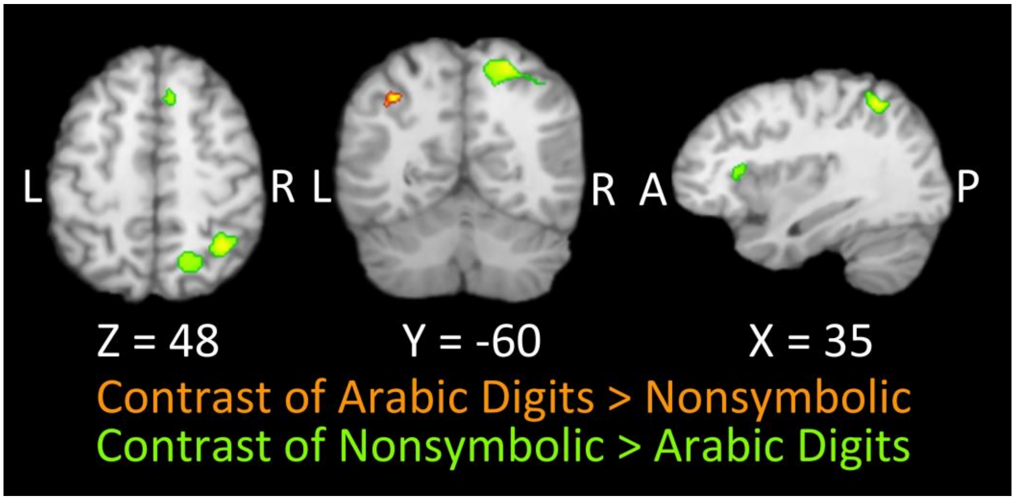

Figure 2.4 ALE maps of contrasts between the Arabic digits and nonsymbolic single dataset ALE maps. ALE contrast analyses reveal specific activation for Arabic digits>nonsymbolic (orange) and nonsymbolic>Arabic digits (green). Contrast analyses were conducted using an uncorrected $p<.01$ with a minimum volume of 50mm^3. Brain slices are shown at coordinates (x, y, z) in Talairach space.

2.3.3 Single Dataset ALE Maps (Passive only)

In order to determine which brain regions support symbolic and nonsymbolic number processing in the absence of task demands, ALE maps were created that only included papers that used passive viewing paradigms (Table 2.7, Figure 2.5).

2.3.3.1 Passive (symbolic and nonsymbolic) ALE Map

The passive single dataset meta-analysis revealed a frontoparietal network of brain areas that qualitatively overlaps with many of the regions that were found in the ALE maps from the conjunction and contrast analyses (Table 2.7, Figure 2.5, Figure 2.6). Specifically, the single dataset ALE map for passive symbolic and nonsymbolic revealed convergence of activation in the left superior parietal lobule, precuneus and middle temporal gyrus, the right inferior parietal lobule and precuneus, and left cingulate gyrus.

2.3.3.2 Passive Symbolic ALE Map

The single dataset meta-analysis for passive symbolic revealed a large cluster of brain activation in the left precuneus and in the left fusiform gyrus (Table 2.7, Figure 2.6).

2.3.3.3 Passive Nonsymbolic ALE Map

The single dataset meta-analysis for passive nonsymbolic revealed brain activation in the right precuneus, superior parietal lobule, and middle occipital gyrus (Table 2.7, Figure 2.6).

Table 2.7 Passive Single Dataset Analyses

Hemisphere	Brain Area	BA	X	Y	Z	ALE	Vol/mm
Symbolic and Nonsymbolic							
L	Precuneus	19	-30	-66	36	0.022	3736
L	Precuneus	7	-22	-66	36	0.015	
L	Superior Parietal Lobule	7	-26	-62	48	0.014	
L	Superior Parietal Lobule	7	-32	-66	52	0.014	
L	Middle Temporal Gyrus	39	-26	-52	34	0.014	
L	Superior Parietal Lobule	7	-30	-54	44	0.012	
R	Precuneus	7	24	-52	48	0.017	2128
R	Inferior Parietal Lobule	40	36	-48	48	0.013	
L	Cingulate Gyrus	24	-8	6	46	0.015	640
Symbolic							
L	Precuneus	19	-30	-66	36	0.014	1016
L	Fusiform Gyrus	37	-46	-48	-12	0.014	560
Nonsymbolic							
R	Precuneus	7	26	-50	50	0.014	1272
L	Superior Parietal Lobule	7	-28	-54	44	0.011	688
L	Superior Parietal Lobule	7	-28	-62	48	0.010	
L	Middle Occipital Gyrus	18	-24	-88	2	0.013	608

X, Y and Z – x,y,z values of the location of the maximum ALE value

ALE - maximum ALE value observed in the cluster

Vol/mm^3 - volume of cluster in mm_3

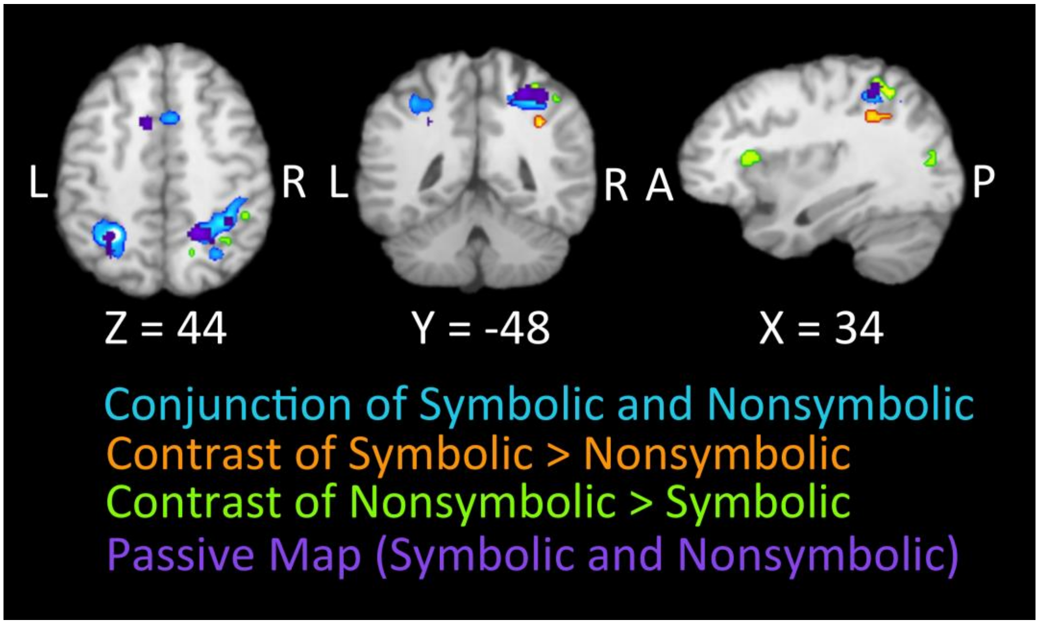

Figure 2.5 Single dataset ALE map using only studies with a passive design (purple) overlaid on top of Figure 2.3. Activations of passive ALE map were identified using a cluster-level threshold of $p<.05$ with 1000 threshold permutations and an uncorrected $p<.001$ Brain slices are shown at coordinates (x, y, z) in Talairach space.

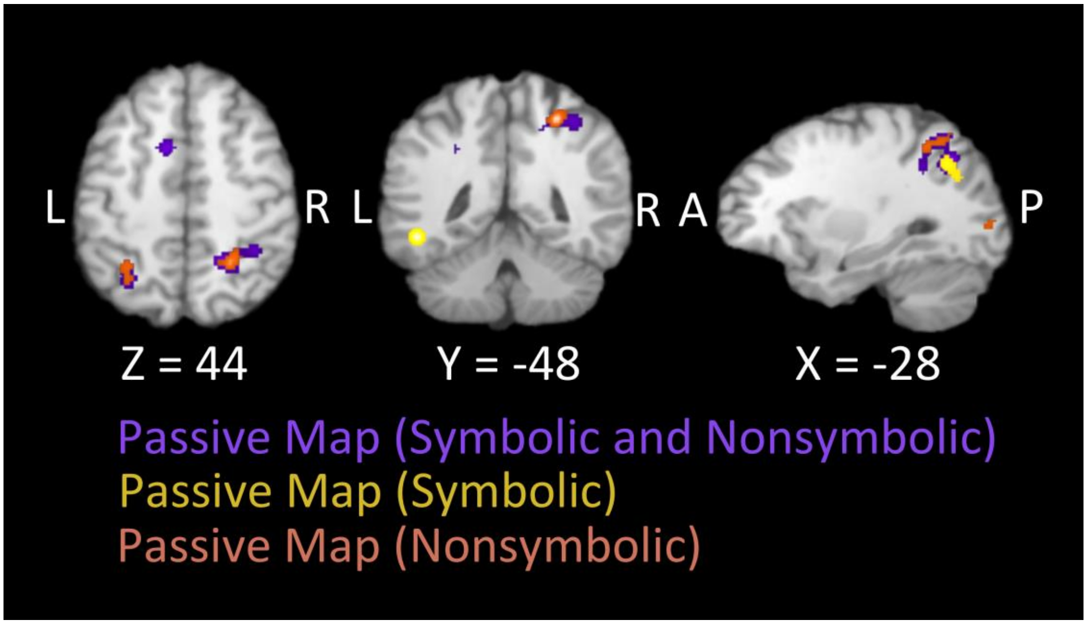

Figure 2.6 Single dataset ALE map of all studies (symbolic and nonsymbolic) that used a passive design (purple). Single file ALE maps of studies using passive designs with symbolic stimuli (orange) and nonsymbolic stimuli (yellow) are overlaid. Activations of passive ALE maps were identified using a cluster-level threshold of *p*<.05 with 1000 threshold permutations and an uncorrected *p*<.001 Brain slices are shown at coordinates (x, y, z) in Talairach space.

2.3.4 Split Half Reliability Analyses

The contrast analyses between symbolic and nonsymbolic ALE maps of activation revealed significant differences between symbolic and nonsymbolic number processing at the meta-analytic level (Table 2.5, Figure 2.3). Follow-up reliability analyses were conducted in order to determine the extent to which the noise in the data can account for some of the between symbolic versus nonsymbolic activations. Specifically, the contrasts that comprise the symbolic and nonsymbolic number processing ALE maps were each split into two random halves (an ALE map of activation was created for each half). A contrast analysis was run in order to determine regions that were significantly more activated for half one>half two and for half two>half one. This analysis was repeated three times for each symbolic and nonsymbolic ALE map. These analyses revealed that for the symbolic ALE reliability analysis, only one of the six contrasts showed a significant difference between half one and half two. However, for the nonsymbolic ALE reliability analysis, five of the six contrasts showed a significant difference between half one and half two (Table 2.8). See Table 2.9 for a description of which brain regions showed significant differences. Table 2.9 reports the random regions that come out when contrasting half of the map against the other half. The regions reported in this table are small and random. The purpose of this table is to detail the regions that came out as significant in the reliability analyses in order to highlight that the regions that were different between the two halves are small and span many different regions across the brain.

Table 2.8 Reliability Analyses: Number of Significant Regions

Run	Contrast	Number of Regions
Symbolic		
Run 1	Half 1 > Half 2	0
	Half 2 > Half 1	1
Run 2	Half 1 > Half 2	0
	Half 2 > Half 1	0
Run 3	Half 1 > Half 2	0
	Half 2 > Half 1	0
Nonsymbolic		
Run 1	Half 1 > Half 2	1
	Half 2 > Half 1	1
Run 2	Half 1 > Half 2	3
	Half 2 > Half 1	1
Run 3	Half 1 > Half 2	1
	Half 2 > Half 1	0

Table 2.9 Reliability Analyses: Location of Significant Clusters

Hemisphere	Brain Area	BA	X	Y	Z	ALE	Vol/mm
Symbolic							
L	Inferior Parietal Lobule	40	-39	-55	36	2.652	216
L	Inferior Parietal Lobule	40	-34	-56	36	2.501	
Nonsymbolic							
L	Middle Occipital Gyrus	18	-36	-86	-2	2.794	464
L	Middle Occipital Gyrus	18	-35	-85	2	2.652	
L	Middle Occipital Gyrus	18	-29	-85	2	2.605	
L	Inferior Occipital Gyrus	18	-25	-89	1	2.382	
L	Precuneus	31	-18	-48	39	3.156	504
L	Superior Parietal Lobule	7	-32	-52	52	2.652	512
R	Precuneus	7	28	-54	50	2.794	144
R	Superior Parietal Lobule	7	26	-52	42	2.468	
R	Precuneus	7	20	-60	42	2.727	120
L	Cingulate Gyrus	32	1	16	39	3.719	640
R	Medial Frontal Gyrus	6	8	16	44	2.418	
L	Superior Parietal Lobule	7	-26	-58	56	2.848	120

X, Y and Z – x,y,z values of the location of the maximum ALE value

ALE – conjunction analysis: maximum ALE value observed in the cluster, contrast analyses: maximum z-score observed in the cluster
Vol/mm^3 - volume of cluster in mm3

2.4 Discussion

The current meta-analysis examined the neural bases of the ability to process symbolic and nonsymbolic numbers. Quantitative meta-analytic techniques were used to address two important questions. First, the study examined whether neural representations of numbers are represented abstractly or if the human brain hosts format-dependent representations for number. This question was addressed by identifying both overlapping and distinct brain regions that are activated by symbolic and nonsymbolic numbers. Second, the study examined whether these converging regions of activation were related to magnitude processing rather than top-down task demands.

The current study represents the first quantitative meta-analysis examining the neural correlates of symbolic and nonsymbolic magnitude processing. Specifically, two ALE meta-analyses were computed to identify the neural correlates of symbolic and nonsymbolic number processing. These meta-analyses revealed that brain regions in the frontoparietal network were associated with symbolic and nonsymbolic number processing across studies. Activation in regions within the bilateral parietal and frontal cortex was correlated with both symbolic and nonsymbolic number processing. The left middle occipital gyrus was activated during symbolic number processing and the bilateral middle occipital gyri were activated during nonsymbolic number processing. The spatial distributions of the single dataset quantitative ALE maps that were generated for symbolic and nonsymbolic numbers suggest that both overlapping and distinct brain regions are associated with symbolic and nonsymbolic numbers.

2.4.1 Symbolic vs. Nonsymbolic

In order to quantitatively address whether numbers are represented abstractly or if the human brain hosts format-dependent representations for number, conjunction and contrast analyses were conducted to compare symbolic and nonsymbolic ALE maps. Conjunction analyses revealed that regions along the bilateral inferior parietal lobules and precuneus, as well as the left superior parietal lobule, and right superior frontal gyrus, were specifically activated by the conjunction of symbolic and nonsymbolic numbers. Contrast analyses revealed that the right supramarginal gyrus and inferior parietal lobule, as well as the left angular gyrus, were specifically activated for symbolic compared to the nonsymbolic numbers. Notably, only the left inferior parietal lobule was significant specifically for Arabic digits compared to nonsymbolic numbers. A right-lateralized frontoparietal network including the right superior parietal lobule, inferior parietal lobule, precuneus, superior frontal gyrus and insula as well as the middle occipital gyrus were specifically activated for nonsymbolic compared to symbolic numbers. These findings are consistent with empirical research suggesting that symbolic and nonsymbolic numbers are processed using both overlapping and distinct neural mechanisms (e.g., Holloway et al., 2010; Lyons and Beilock, 2013; Piazza et al., 2007).

In addition to quantitatively replicating the finding that overlapping and distinct neural populations support different number formats, these conjunction and contrast analyses provide valuable insights into the highly debated question of whether number is processed abstractly (e.g., Ansari, 2007; Cohen Kadosh and Walsh, 2009; Cohen Kadosh et al., 2007; Dehaene et al., 1998; Nieder and Dehaene, 2009; Piazza et al., 2007). The finding that several neural regions were activated by the conjunction of symbolic and nonsymbolic number maps supports the notion that the human brain represents numbers abstractly. This finding implicates the bilateral inferior parietal lobules and precuneus, as well as the left superior parietal lobule, and right superior frontal gyrus, as candidate regions that may support abstract number processing. However, the nature of the overlap between symbolic and nonsymbolic numerical maps is unclear because the statistical algorithms that underlie ALE do not evaluate patterns of activation within overlapping regions. Therefore, while it is possible that the overlap could represent common semantic processing, the overlap could also represent common task demands such as attention or response-selection. In empirical studies, researchers addressed this limitation of coarse spatial resolution by implementing multi-voxel pattern analysis (MVPA) to examine patterns of activation for symbolic and nonsymbolic numbers in the intraparietal sulcus (Damarla & Just, 2013; Eger et al., 2009; Lyons et al., 2014) and at the whole-brain level (Bulthé et al., 2014). These studies consistently reported a lack of association between patterns of activation for symbolic and nonsymbolic number processing. Such findings challenge the idea that overlapping activation for symbolic and nonsymbolic numerical processing implies that numbers are processed abstractly. It is important to interpret overlapping activation with caution until data-analysis techniques become available that can analyze patterns of activation across multiple studies.

Meta-analytic contrast analyses revealed that distinct neural mechanisms are activated by symbolic compared to nonsymbolic numbers and supported the theory that numerical representations are dependent on format (Cohen Kadosh et al., 2011, 2007; Cohen Kadosh & Walsh, 2009). In particular, the contrast symbolic>nonsymbolic revealed activation in the right supramarginal gyrus and the inferior parietal lobule, as well as the left angular gyrus. Conversely, the contrast nonsymbolic>symbolic showed that nonsymbolic numbers correlate with activation in the right superior parietal lobule, inferior parietal lobule, and precuneus (as well as right-lateralized regions not in the parietal cortex including the insula, superior frontal gyrus, and middle occipital gyrus). Interestingly, regions specifically activated by either symbolic or nonsymbolic stimulus formats seemed to be lateralized within the parietal cortex. Specifically, the right parietal lobule supported both symbolic and nonsymbolic specific processing, while activation in the left parietal lobule was specific to symbolic number processing. However, even though symbolic and nonsymbolic maps both show activation in the right parietal cortex, the localization in the right parietal lobe is different. Specifically, activation nonsymbolic>symbolic activation is more superior, while symbolic>nonsymbolic activation more inferior. In other words, the contrast analyses comparing symbolic and nonsymbolic ALE maps suggest that within the right parietal cortex, symbolic and nonsymbolic number processing are associated with different spatial patterns of activation.

The symbolic ALE map included several symbolic number formats: Arabic digits, written number words, and verbal number words. In contrast, the nonsymbolic ALE map included only visual displays of arrays of objects. One potential explanation for the significant activation revealed by the contrast analyses is that the symbolic number map consists of not only of visual but also written and auditory stimuli. To test this, a single file ALE map with only Arabic digits was created and compared to the nonsymbolic map. This contrast analysis revealed that the processing of Arabic digits correlated with activity in only the left inferior parietal lobule while processing nonsymbolic numbers correlated with activity in the right superior parietal lobule, insula and medial frontal gyrus. Therefore, the left inferior parietal lobule may be specific to the processing of Arabic digits, while the right supramarginal gyrus and inferior parietal lobule may host more abstract symbolic number representations. The finding that the symbolic passive map reveals left-lateralized parietal activation provides converging evidence supporting the notion that the left inferior parietal lobe is important for symbolic number representations.

Significantly, a majority of the papers that were included in the ALE meta-analyses used visual stimuli. Analyzing overlapping and distinct activation for number processing tasks, measured using different modalities at the meta-analytic level, would aid in evaluating abstract number representations. To date, there are not enough studies that measure number in the verbal, or tactile domains to form an ALE map that can be contrasted against a visual number processing map. Consequently, additional empirical research is necessary to investigate the neural correlates of number processing in non-visual domains.

In addition to these differences in brain activation, a reliability analyses revealed that the nonsymbolic ALE map has more variability than the symbolic ALE map. More specifically, we examined the extent to which there were significant differences within formats, by randomly splitting the included contrasts in half and contrasting the two halves. One would predict that if the activations are highly consistent, then no differences in such an analysis should be observed. While we found this to be the case for symbolic number processing, the analyses of the nonsymbolic data revealed some significant variability. Specifically, the split half analysis of the nonsymbolic data revealed that in five out of the six contrasts revealed greater activation in one half of the nonsymbolic dataset compared to the other half. Given that the data were randomly split, conclusions regarding the potential processing differences between the two halves of the data cannot be made. However, it should be noted that the significant regions within the reliability analyses did not reveal systematic locations (i.e., there were regions across the frontal, parietal, and occipital lobes). This suggests that the lack of reliability in the nonsymbolic map was due to variable data across studies rather than systematic variability within specific brain regions.

The finding from the reliability analyses indicate, that the symbolic ALE map is more reliable than the nonsymbolic ALE map when using equivalent numbers of papers, and the same thresholds suggest that this distinction is a predicament of the data in the field rather than the methodology of the meta-analyses. This finding of differences in the reliability of the symbolic and nonsymbolic map should be taken into account when considering the results of contrast analyses contrasting symbolic and nonsymbolic ALE maps. Specifically, regions that are more activated by nonsymbolic numbers compared to symbolic numbers should be interpreted with caution within the context of the current meta-analysis. Additionally, this finding should be considered when evaluating brain regions that correlate with nonsymbolic number processing within empirical studies. Overall, these reliability data provide valuable insights into underlying differences between format-dependent neural responses and set the foundation for future empirical research which needed to disentangle the difference in variability between symbolic and nonsymbolic number processing at the meta-analytic level.

The findings that symbolic numbers activated the bilateral inferior regions of the parietal lobe while nonsymbolic numbers activated right-lateralized superior regions of the parietal lobe conflicts with the notion that the brain processes numbers using only a number module that is indifferent to number format. Instead, regions that are format-specific may imply differential semantic processing of symbolic and nonsymbolic numbers. However, as meta-analyses do not include experimental manipulations, they cannot determine what brain regions sub-serve specific processes. This is important to consider with respect to the current meta-analytic contrasts because these contrasts alone cannot confirm that the areas revealed are really engaging in format-specific semantic processing. These regions of activation may reflect other processes that differ between formats. Although it is possible that specific regions activated by symbolic>nonsymbolic and nonsymbolic>symbolic reflect something other than format-specific processing, there are several aspects of the analysis that speak against this. First, all contrasts that were entered into the single file ALE maps contrast basic number processing against a control task that was matched in terms of perceptual and other non-semantic processing dimensions. Second, the symbolic and nonsymbolic passive ALE maps show similar differences. This suggests that the regions that are specifically activated by symbolic and nonsymbolic number processing are likely related to semantic differences between symbolic and nonsymbolic number processing. Ultimately, this question of format specificity in the human brain calls for further experimental investigation in order to understand the process of how the brain represents symbols compared to nonsymbolic numbers. In this way, the present meta-analysis may pave the way for new investigations into the specific nature of format-specific processing in the parietal cortex.

The concept of format-specific hemispheric specialization within the parietal lobes has previously been supported by developmental studies (e.g., Holloway and Ansari 2010). For example, researchers revealed increasing specialization of the left intraparietal sulcus for processing of symbolic numbers across development (e.g., Vogel et al. 2014) but consistent activation across children and adults in the right intraparietal sulcus for nonsymbolic numbers (e.g., Cantlon et al., 2006). The idea that this hemispheric asymmetry in the parietal cortex is a result of developmental specialization is further supported by a developmental quantitative meta-analysis that identified brain regions supporting symbolic and nonsymbolic number processing in children (Kaufmann et al. 2011). The results of this meta-analysis showed that the notation of the number (symbolic vs. nonsymbolic) influenced the location of neural activation patterns both within and outside the parietal lobes (Kaufmann et al. 2011). In accordance with the current meta-analyses, Kaufmann et al., (2011) showed that symbolic number magnitude processing was correlated with bilateral parietal activation while activation during nonsymbolic number processing was lateralized to the right parietal lobe. Together, these findings challenge the notion that the parietal cortex hosts a single system that processes number abstractly. Instead, it is probable that hemispheric specialization for number formats in the parietal cortex emerges over the course of development.

Beyond the parietal cortex, it has long been predicted that the ventral visual stream might house a number form area (NFA, Dehaene and Cohen 1995). In support of this prediction, the ALE passive symbolic map revealed activation in the ventral stream. However, contrary to this prediction, the contrast of symbolic > nonsymbolic in the present meta-analysis did not reveal regions in the ventral visual stream that were more active for symbolic than nonsymbolic processing of number. Therefore, this meta-analysis does not lend strong support to the NFA as no contrasts were able to reveal symbolic-specific activation. Recently, the existence of an NFA in the ventral stream was revealed using intracranial electrophysiological recording (Shum et al., 2013). This study also reported evidence to suggest that the region that was shown to exhibit category-selectivity for numerals is located within or near a zone in which there is a drop-out of the fMRI signal due to the auditory canal and venous sinus artifacts. Indeed, a recent study in which this fMRI signal drop out was reduced revealed category selectivity for numerals in bilateral regions of the inferior temporal gyri (Grotheer, Herrmann, & Kovacs, 2016). It is possible, therefore, that the absence of evidence for an NFA in the current meta-analysis stems from an fMRI signal drop out masking category-selective activation for numerals in the ventral stream. Having said that, the evidence for the existence of an NFA is, to date, sparse and there is a need for more evidence using methods that control for the fMRI signal drop out in the inferior temporal gyrus. Once sufficient evidence has been accumulated, a meta-analytic approach, such as the one used in the present paper could be employed to quantify the consistency of evidence for the existence of the NFA.

2.4.2 The Three Parietal Circuits Model

Several different theories of numerical cognition propose potential mechanisms that may underlie mathematical abilities (Campbell, 1994; Dehaene et al., 2003; McCloskey, 1992). Among these theories is the three parietal circuits model (Dehaene et al., 2003) which is distinct from other theories because it makes specific predictions about the neuroanatomical underlying number processing. This is an influential, highly cited model that is often claimed to be predictive of empirical data (e.g., Neumärker 2000; Schmithorst and Brown 2004). The current meta-analysis has the potential to further constrain existing theories, such as the three parietal circuits model, that propose potential mechanisms that underlie basic number processing. The three parietal circuits model (Dehaene et al., 2003), predicts that three distinct systems of representation are recruited for basic numerical processing and calculation tasks. These systems include a quantity system (which processes abstract numerical representations that are not related to number format), a verbal system (which represents numbers as words) and a visual system (which encodes numbers as strings of Arabic digits). Dehaene et al., (2003) used three-dimensional visualization software to examine how parietal activation related to this model. Using these qualitative meta-analytic data, they proposed that three distinct, but functionally related networks coexist in the parietal lobes and that these networks are used to support numerical processing. Briefly, the three parietal circuits model suggests that the bilateral horizontal segments of the intraparietal sulci are related to the quantity system, the left angular gyrus is related to the verbal system, and the posterior superior parietal lobules are related to the visual system, and specifically, attention processes. For over a decade, this model has driven researchers to examine the neural underpinnings of basic number processing and calculation. This influential model has been both supported and challenged by empirical research (Chassy & Grodd, 2012; Eger et al., 2003; Piazza et al., 2004, 2007; Price & Ansari, 2011). Results of the current quantitative meta-analysis challenge several aspects of the three parietal circuits model. First, the finding from the conjunction analysis that reveals that both symbolic and nonsymbolic number processing activate the regions in the bilateral inferior parietal lobules and precuneus, and left superior parietal lobule challenges the notion put forward by Dehaene et al., (2003) that "the horizontal segment of the intraparietal sulcus (HIPS) appears as a plausible candidate for domain specificity" (p.487). Second, the finding that the left angular gyrus was specifically activated for symbolic numbers supports the idea that the left angular gyrus is related to the verbal system. This was supported by the contrast analysis from the current meta-analyses. However, the right supramarginal gyrus and inferior parietal lobule were also activated by symbolic>nonsymbolic number processing. Therefore, although it is possible that the activation in the left angular gyrus is related to the verbal system, which is likely used more by symbolic compared to nonsymbolic number processing, the activation in the right parietal lobe does not fit with this account. An alternative explanation is that these bilateral parietal regions are part of a format-specific number-processing region for symbolic number processing. Specifically, perhaps the left angular gyrus supports the verbal aspects of number processing while the right supramarginal gyrus and inferior parietal lobule support other aspects of symbolic number processing. In lieu of these results, perhaps the left angular gyrus supports the verbal processing and reading of symbols whereas the right supramarginal gyrus and inferior parietal lobule support processes that use this verbal symbolic knowledge and attentional processes to perform higher-level tasks such as calculation. This suggestion is consistent with results from the calculation meta-analysis (Arsalidou & Taylor, 2011), which report that the right angular gyrus is activated during calculation. Third, findings from the current meta-analysis both support and challenge the idea that activation in the superior parietal lobules is a consequence of attending to visual dimensions of numbers. Evidence from the conjunction analyses of the current meta-analyses showed that the left superior parietal lobule was activated for the conjunction of symbolic and nonsymbolic magnitude processing. Therefore, based on these findings, the left superior parietal lobule is an equally plausible candidate for domain specificity of number processing. Although, this convergence of activation could be due to a visual attention orienting response as proposed by Dehaene et al., (2003), the left superior parietal lobule was also found in the passive meta-analysis. Thus, there is superior parietal lobule activation even when the task demands, and therefore the attentional demands, are reduced. Importantly, the fact that nonsymbolic>symbolic was correlated with activation in the right superior parietal lobule conflicts with the idea that the superior parietal lobule supports only visual attention processes. Instead, these findings reveal hemispheric asymmetry in the bilateral superior parietal lobules that might suggest that the right superior parietal lobule hosts format-dependent representations of nonsymbolic numbers and the left superior parietal lobule hosts and abstract number processing region. One possible explanation for this finding is that the right superior parietal lobule is specifically correlated with visual attentional processes associated with nonsymbolic number tasks. Another possible explanation for the format-specific activation of the right intraparietal sulcus is that this region is associated with processes that are specific to nonsymbolic numerical magnitude processing. Using a computational model, Verguts and Fias (2004) trained a neural network to map a symbolic or nonsymbolic numerical visual input onto a place-coded representation. Place-coding is a way of representing the cardinal value of the total number of items in a set by representing the quantity of the set as a place on a number line. In the computational model, symbolic inputs are mapped directly onto a place-coding representation. However, nonsymbolic inputs undergo an intermediate step between the nonsymbolic visual input and a place-coding representation. This intermediate step is referred to as summation coding. In summation coding, the size of the neural representation monotonically varies with the number of objects being presented. During this intermediate step, neurons accumulate proportionally to the number of objects that were visually processed. A large body of neuroscience evidence converges with these computational models suggesting that place-coded neurons exist within the primate brain (for review see, Nieder and Dehaene, 2009 or Nieder, 2013). These studies typically use single-cell recordings, monitoring individual neurons, while non-human primates discriminate between nonsymbolic arrays (e.g., Nieder and Miller, 2004; Nieder and Miller, 2003; Tudusciuc and Nieder, 2007). Overwhelming evidence indicates that the primate brain place codes numerosity (Nieder & Miller, 2004; Okuyama, Kuki, & Mushiake, 2015) even in monkeys that were never trained to discriminate numbers (Viswanathan & Nieder, 2013). Converging evidence from human fMRI adaptation studies revealed that tuned number neurons respond to dot arrays (Jacob & Nieder, 2009; Piazza et al., 2004). These tuned number neurons mirror place-coding neurons within the non-human primate brain (Jacob & Nieder, 2009).

Additionally, the existence of this type of summation coding has been found in humans both behaviourally (Roggeman, Verguts, Fias, Vergutsa, & Fias, 2007) and at the neuronal level (Roggeman, Santens, Fias, & Verguts, 2011; Santens et al., 2010). In particular, neuroimaging studies have identified the right superior parietal lobule as a potential region that might support the process of accumulation during summation coding (Roggeman et al., 2011; Santens et al., 2010). Therefore, one possible explanation for activation in the right superior parietal lobule relating specifically to nonsymbolic number processing is that this region supports summation coding. Ultimately, these meta-analytic findings question the idea that the intraparietal sulcus hosts a system that processes numbers abstractly and the superior parietal lobule solely supports visual attentional processing.

It has been over a decade since the initial proposal of the three parietal circuits model. The results of the current quantitative meta-analysis do not converge with the data that support the three parietal circuits model (Dehaene et al., 2003). On the basis of these discrepancies, it is recommended that the three parietal circuits model should be updated. The parietal lobules should be canvased in search of regions that support both format-dependent and format-independent numerical representations. This will illuminate the extent to which format-specific regions reflect various components of format-specific processing including semantic, perceptual and decision-making processing. Furthermore, the examination of brain regions that support format-dependent and format-independent numerical representations will clarify which regions in the intraparietal sulcus, inferior parietal lobule and superior parietal lobule are associated with various aspects of basic magnitude processing. This should ultimately illuminate the mechanism underlying magnitude processing in the parietal lobes.

2.4.3 Frontal vs. Parietal

During the last decade, there has been an intense focus on the parietal lobes as brain regions involved in number processing (e.g., Dehaene et al. 2003; Eger et al. 2003; Fias et al. 2003; Cohen Kadosh et al. 2007; Cohen Kadosh and Walsh 2009). However, many neuroimaging studies reported activation in regions of the frontal cortex during number processing (e.g., Eger et al. 2003; Cohen Kadosh et al. 2007; Franklin and Jonides 2008; Cohen Kadosh and Walsh 2009; Dormal and Pesenti 2009; Dormal et al. 2012; Hayashi et al. 2013). The importance of the frontal cortex in number processing was revealed in research that used single-cell recordings in animals as well as in pediatric neuroimaging studies. Specifically, invasive single-cell recordings in non-human primates identified putative 'number neurons' in the parietal as well as the prefrontal cortex; these neurons responded to specific quantities (such as two dots) while animals performed a numerical discrimination task (Nieder, 2013; Nieder et al., 2002). These findings suggested that regions of the frontal cortex may host pure magnitude representations. Similarly, pediatric neuroimaging studies showed that young children recruited the prefrontal cortex more than adults during number discrimination tasks. In contrast, intraparietal sulcus activation during number comparison increased across development (Ansari et al., 2005; Kaufmann et al., 2006). Researchers suggested that this frontal to parietal shift from childhood to adulthood may reflect a decrease in the need for domain-general cognitive resources such as working memory and attention as children begin to process number symbols automatically (Cantlon et al., 2006; Cantlon, Libertus, et al., 2009; Venkatraman et al., 2005). The notion that regions in the frontal cortex are still important for number and calculation tasks among adults is further supported by a quantitative meta-analysis that identified brain regions supporting number processing and calculation in adults (Arsalidou & Taylor, 2011). Unlike the current meta-analysis, Arsalidou and Taylor, (2011) focused on calculation tasks such as arithmetic and subtraction tasks. Their meta-analysis showed that prefrontal regions are essential for number and calculation. Moreover, they revealed that activation in regions along the prefrontal cortex was related to the difficulty of the task. Specifically, IFG was activated during the processing of simple numerical tasks while the MFG and superior frontal gyrus were involved in more complex calculation problems (Arsalidou & Taylor, 2011). In view of this, Arsalidou and Taylor, (2011) suggested that this activation in the prefrontal cortex was a result of domain-general processes, such as working memory, that are essential for number and calculation tasks. A common explanation for the consistent activation reported in the frontal cortex during number and calculation tasks was that the frontal cortex is activated in response to general cognitive processes associated with the task (e.g., Cantlon et al. 2006; Arsalidou and Taylor 2011). However, it has also been argued that frontal activation is supporting number representations rather than general cognitive processes (for a review see: Nieder and Dehaene, 2009).

The current meta-analysis lends additional support to the idea that frontal activation is important for number processing during basic number tasks. Results revealed consistent activation in frontal regions during symbolic and nonsymbolic number processing. Moreover, results showed that neural activation in response to number processing is no less consistent in the frontal cortex than in the parietal cortex. In particular, the single dataset ALE maps revealed that the superior frontal gyrus was consistently activated during symbolic magnitude processing and the right medial frontal gyrus and cingulate gyrus were activated during nonsymbolic magnitude processing. The right superior frontal gyrus was also activated in the conjunction analysis of symbolic and nonsymbolic and specifically for nonsymbolic number processing the contrast analyses comparing nonsymbolic>symbolic. The current meta-analysis deliberately included only basic magnitude processing tasks in order to minimize the recruitment of additional cognitive resources typically needed for complex calculation tasks. Additionally, all contrasts included in the current meta-analysis were contrasted against control conditions. These attributes make it likely that the activation revealed in the current meta-analyses is related, at least in part, to magnitude representations. The superior frontal gyrus was also found to activate to complex calculation tasks (Arsalidou & Taylor, 2011), however the location of activity differs such that complex calculations elicit activity in anterior parts of the superior frontal gyrus (BA 10), whereas basic number tasks elicit activity in superior frontal gyrus (BA 6), a region often associated with the premotor cortex. Further evidence for the idea that the frontal cortex may support magnitude representations comes from the contrast analyses, which revealed that the right superior frontal gyrus was specifically activated by nonsymbolic numbers but not by symbolic numbers. The specificity of frontal activation for nonsymbolic numbers suggests that this right-lateralized frontal region may be essential for identifying the number of objects within a set. Therefore, similarly to activation in the parietal cortex, the activation patterns within the frontal cortex vary as a function of format (symbolic vs. nonsymbolic). Together, the data from the current meta-analysis offer no reason to think that the parietal cortex is more specialized for number than the frontal cortex.

Although the pattern of frontal activation suggests that the superior frontal gyrus may support basic number processing, the fact that many of the studies included in the symbolic and nonsymbolic meta-analyses were active tasks, and therefore had general cognitive processes such as decision-making, precludes the conclusion that the superior frontal gyrus supports magnitude representations rather than general cognitive processes. To overcome this limitation, single file ALE meta-analyses were computed to examine converging activation of studies that used passive tasks. These single file passive maps are essential to illuminate which brain regions are activated by responding to a task. The brain activation that was associated with passive symbolic and nonsymbolic numerical tasks was consistent with activation revealed in the ALE contrast maps comparing symbolic and nonsymbolic maps of activation that included both passive and active tasks. Specifically, both the active and passive maps and passive only maps revealed bilateral activation in the left superior parietal lobule and precuneus and the right inferior parietal lobule and precuneus as well as the left cingulate gyrus for symbolic and nonsymbolic number processing. Although the current study did not have enough power to statistically contrast the passive symbolic and passive nonsymbolic maps, the qualitative comparison of the passive symbolic and passive nonsymbolic single file ALE maps depicted in Figure 2.6 is consistent with the contrast analyses symbolic>nonsymbolic and nonsymbolic>symbolic. Specifically, the passive symbolic map reveals activation in the left precuneus and the left fusiform gyrus and the passive nonsymbolic ALE map reveals activation in the right precuneus, left superior parietal lobule, and left middle occipital gyrus. The cluster of activation is larger in the right parietal lobule compared to the left parietal lobule. Therefore, similarly to the contrast analyses that included both passive and active conditions, a qualitative comparison of passive symbolic and passive nonsymbolic single file ALE maps reveals trends of lateralization. Specifically, passive single file ALE meta-analyses suggest that symbolic numbers activate the left parietal lobe and nonsymbolic numbers activate a larger region in the right parietal lobe. Therefore, the passive maps reflect similar patterns of activation to the active and passive single dataset maps as well as the contrasts for both symbolic and nonsymbolic number processing. Together, these passive maps suggest that activation in the bilateral parietal cortex and the left cingulate gyrus may be related to format-dependent and independent magnitude processing, rather than task demands.

Taken together, the present meta-analysis does not support the argument that frontal regions are involved in task demands while parietal regions are involved in semantic processing. Instead, these data indicate that both the frontal cortex and the parietal cortex may be involved in general cognitive processes associated with number tasks and magnitude representations. Ultimately, the field of numerical cognition needs to acknowledge that frontal regions are consistently engaged, even during basic number processing, and in accordance with this, reduce biases towards parietal activation.

2.4.4 Limitations and Advantages of ALE

As the present study used ALE methodology, it is important to note several specific limitations with ALE such as difficulty accounting for differences in statistical thresholding approaches across studies and difficulty determining the spatial extent and magnitude of the activation for each focus (for a more detailed discussion of these limitations: Ellison-Wright et al. 2008; Christ et al. 2009; Di Martino et al. 2009; Arsalidou and Taylor 2011). Additionally, as ALE uses data from fMRI and PET studies, it is important to consider that the blood-oxygen-level-dependent (BOLD) signal and the PET signal are indirect signals. Specifically, the PET signal and BOLD response estimate brain activity by detecting changes associated with blood flow (Logothetis, 2003). Moreover, these indirect signals are typically corrected for motion, smoothed, and averaged across participants. Therefore, at best, these signals only reveal mass activation of a brain region, and not individual neuronal firing (see Scott and Wise, (2003) for a more detailed critical appraisal of functional imaging). Since fMRI and PET detect an indirect mass signal that is smoothed across a large number of neurons in the brain and averaged across subjects, it is likely that one region of activation within a single empirical study, represents several neural networks (Nieder, 2004). This idea is supported by data in primates that revealed that less than 20% of neurons in the intraparietal sulcus responded to numbers (Nieder and Miller, 2004). This is particularly important to consider when examining which brain regions support numbers abstractly versus a format-dependent manner. Therefore, when interpreting the results of the current meta-analysis, it is perhaps more accurate to argue that regions which seem to process numbers abstractly contain a larger number of "abstract number-selective neurons," whereas regions that are sensitive to number format have a larger number of "format-dependent number-selective neurons." As the field of functioning imaging develops, future research will be needed to more precisely examine abstract and format-dependent regions at the neuronal level in humans.

Despite these limitations, ALE has several important advantages as a tool for synthesizing neuroimaging data. Particularly, the algorithms that underlie ALE allow for the quantification of foci among empirical papers with varying methodologies. For example, this method can account for differences in the number of runs, the duration of the presentation of the stimuli and the type of design (e.g., block vs. event-related). It is likely that this diversity in methodologies is one of the main drivers of conflicting findings often reported between studies. Additionally, because neuroimaging research is so costly, the majority of empirical studies have small sample sizes. ALE groups different studies with varying methodologies by domains in order to increase sample sizes and ultimately address broader theoretical questions. Overall, ALE is a valuable meta-analytic tool that can quantitatively integrate large amounts of neuroimaging data to reveal converging patterns of findings.

2.4.5 Conclusions

In conclusion, this meta-analysis has reaffirmed the body of research suggesting that the ability to process numbers relies on a large number of brain regions. This quantitative meta-analysis shows that overlapping and distinct regions in the frontal and parietal lobes are activated by symbolic and nonsymbolic numbers, revealing the specific roles of parietal and frontal regions in supporting number processing. The finding that several neural regions were activated by the conjunction of symbolic and nonsymbolic number maps supports the notion that the human brain represents numbers abstractly. This study also illuminates the lateralization of symbolic compared to nonsymbolic number processing within the parietal lobes. Specifically, the left angular gyrus is potentially important for the mapping of symbols onto quantities (nonsymbolic numbers) while the right superior parietal lobule may be important for processing nonsymbolic sets of items. The lateralization of symbolic and nonsymbolic number is an intriguing avenue for future research. Additionally, this research highlights the consistency of activation within the frontal cortex during number processing. Ultimately, the current meta-analysis extends our understanding of the brain regions associated with basic number processing and initiates future research on the neural mechanisms that underlie our essential ability to comprehend numbers.

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Chapter 3

3 Symbols are Special: An fMRI Adaptation Study of Symbolic, Nonsymbolic and Non-numerical Magnitude Processing in the Human Brain

3.1 Introduction

Humans have the exceptional ability that emerged over the course of human cultural history, to represent numbers symbolically (e.g.,'3' or 'three'). This capacity to represent numbers symbolically is necessary for mathematical thinking, which is a major pillar of contemporary civilization. The uniquely human ability to process these symbolic numerical magnitudes is thought to be supported by the same brain regions that are associated with a pre-existing, innate and evolutionarily ancient abstract number processing system used to process nonsymbolic numerical magnitudes (e.g., three dots '●●●'), in human adults (Brannon, 2006; Dehaene, 2007; Dehaene et al., 2003; Nieder & Dehaene, 2009). However, a growing body of recent evidence suggests that the neural systems used to process symbolic and nonsymbolic numerical magnitudes are more distinct than has been previously assumed (Ansari, 2007; Bulthé, De Smedt, & Op de Beeck, 2014; Cohen Kadosh & Walsh, 2009; Lyons, Ansari, & Beilock, 2012, 2014; Lyons & Beilock, 2013; Sokolowski & Ansari, 2016), thus conflicting with the notion that numbers are processed entirely abstractly. Despite years of research, and a recent meta-analysis of neuroimaging papers, presented in Chapter 2 of the current thesis (Sokolowski, Fias, Mousa, & Ansari, 2017), there remains no clear conclusion about whether symbolic and nonsymbolic numerical magnitudes are supported by the same or distinct brain regions.

Research examining whether symbolic and nonsymbolic numerical magnitudes are represented in the same way in the adult human brain is further complicated by the fact that nonsymbolic numerical magnitudes are inherently confounded by non-numerical magnitudes. For example, physical size is related to nonsymbolic magnitude processing because more objects take up more space. More specifically, a set of six objects takes up more physical space than a set of five of the same sized objects (For review see:

Leibovich & Henik, 2013). Additionally, brain regions associated with numerical magnitude processing are also activated during the processing of non-numerical magnitudes such as physical size, duration, and luminance (Cantlon, Platt, & Brannon, 2009; Cohen Kadosh, Lammertyn, & Izard, 2008; Sokolowski, Fias, Bosah Ononye, & Ansari, 2017; Walsh, 2003). This finding of common brain regions supporting numerical and non-numerical magnitude processing has been taken to suggest that the neural system that has been identified as an abstract number processing system (used to process both symbolic and nonsymbolic numerical magnitudes) may, in fact, be a general system used to process both numerical and non-numerical magnitudes. However, it is clear that previous studies have not sufficiently controlled for continuous properties of the nonsymbolic stimuli. Therefore, the question of whether symbolic and nonsymbolic numerical magnitudes are processed using the same system while controlling for brain regions associated with non-numerical magnitude processing, must still be addressed.

More problematic still is the use of active tasks in the vast majority of studies that compare the neural correlates of symbolic and nonsymbolic numerical thinking. In active tasks, it is notoriously difficult to discern whether neural activation is associated with processing the magnitude of the stimulus or with decision making and motor processing required to complete the active task (Göbel et al., 2004). Additionally, it is challenging to equate difficulty levels on active tasks, which means that a comparison of task effects of active tasks may reflect relative levels of difficulty rather than representational differences between the tasks. To overcome these limitations of active tasks, a small subset of research has used functional Magnetic Resonance Imaging adaptation (fMR-A). fMR-A is a passive design that measures the neural correlates associated with stimuli of interest without requiring participants to make a decision or motor response. This task relies on the principle that neural populations habituate (i.e., adapt) their activity following repeated presentations of the same stimulus (Grill-Spector et al., 2006). In fMR-A paradigms, a particular stimulus (i.e., the habituation stimulus) is repeatedly presented to evoke adaptation of brain regions associated with encoding this stimulus. Following this period of adaptation, a stimulus that differs in some way from the habituation stimulus (i.e., a deviant stimulus) is presented. The presentation of the deviant stimulus results in a rebound of activation in regions that are associated with the attributes of the particular deviant compared to the habituation stimulus. This rebound of activation in response to a deviant stimulus is referred to as the 'neural rebound effect'. The extent of the neural rebound effect in response to a deviant is a function of the difference between the adapted stimulus and the deviant. For example, within the number domain, if a participant is adapted to symbolic number '6' the neural rebound effect will be greater for a symbolic number deviant stimulus that is farther from the adapted stimulus (e.g.,'9') compared to a symbolic number that is closer to the adapted stimulus (e.g.,'7'). The use of fMR-A is necessary to identify whether symbolic and nonsymbolic numerical magnitudes are sub-served by the same neural systems, in human adults.

Using fMR-A, researchers have found that the left inferior parietal lobule responds to processing the magnitude of number symbols (Cohen Kadosh, Cohen Kadosh, Kaas, Henik, & Goebel, 2007; Damarla & Just, 2013; Holloway, Battista, Vogel, & Ansari, 2013; Notebaert, Nelis, & Reynvoet, 2011; Piazza, Pinel, Le Bihan, & Dehaene, 2007; Vogel et al., 2017), whereas bilateral regions in the parietal lobes respond more to nonsymbolic numerical magnitudes (Damarla & Just, 2013; Demeyere, Rotshtein, & Humphreys, 2014; Piazza et al., 2004; Roggeman et al., 2007). Problematically, most previous research only includes a symbolic or a nonsymbolic condition, but not both conditions. In the few studies that examined the passive processing of both symbolic and a nonsymbolic numerical magnitudes using fMR-A (Damarla & Just, 2013; Piazza et al., 2007; Roggeman et al., 2007), participants were adapted to either symbolic numbers and then presented with nonsymbolic deviants, or were adapted to nonsymbolic numbers and then presented with symbolic deviants. This cross-format adaptation can allow researchers to make inferences about whether representations of one format is generalizable to another. For example, the finding that the neural distance effect of one format is also activated by a cross-format deviant might suggest a reliance on the same underlying representations. However, this cross-notation adaptation paradigm cannot reveal whether similar brain regions are adapted to symbolic and nonsymbolic stimuli. This is because in the two conditions compared (symbolic vs. nonsymbolic), the stimuli to which the participant is adapted to are different. Consequently, the finding of overlapping representations using cross-format effects may be driven by a common representation or by the activation of a mechanism that allows for the translation of representations. To directly compare the passive processing of symbolic and nonsymbolic numerical magnitudes using an fMR-A paradigm, it is necessary to adapt the brain to both symbolic and nonsymbolic stimuli, simultaneously. To do this, the habituation stimuli for symbolic and nonsymbolic number processing must be identical.

In this study, we address the fundamental question of whether the culturally acquired, uniquely human, ability to process numbers symbolically is underpinned by the same brain regions that are activated during the processing of nonsymbolic quantities and physical size. This will identify whether different number formats are processed abstractly, using a single system, or in a format-dependent way in the human adult brain. In the present preregistered study (https://osf.io/jrmpf/register/5771ca429ad5a1020de2872e), we develop and implement parallel fMR-A to isolate and directly compare the neural representations of symbols, quantities, and physical size. Importantly, our design controls for brain activations associated with other conditions in the paradigm, as well as inherent confounds associated with active tasks (Grill-Spector et al., 2006). Specifically, in our parallel fMR-A design, participants are repeatedly presented with a specific quantity of the same symbolic number in a white coloured font of a specific size. This set of symbols will be referred to as an 'array'. Following this, one aspect of the array is changed (either the symbol, the quantity, or the size) while the other aspects remain constant. This design allows us to identify whether the culturally acquired ability to process symbolic numerical magnitudes activates the same brain regions that are activated during the processing of nonsymbolic numerical magnitudes and/or non-numerical magnitudes, in the adult brain.

3.2 Methods

3.2.1 Participants

Fifty-two healthy adult participants from London, Ontario, Canada participated in the fMR-A experiment. Our final sample included 45 participants ($Mean_{\text{Age}}$ = 23.6, $Standard\ Deviation_{\text{Age}}$ = 4.3, Age Range = 18-39; 30 women and 22 men), all of whom did not exceed our motion cut-offs (i.e., no overall deviation greater than 3 mm from the 1st volume acquired within a run, and no deviation greater than 1.5 mm between subsequent volumes) and our accuracy cut-offs (Vogel et al., 2015). Accuracy was determined by asking participants to press a predefined button with their right index finger when the numbers appeared in blue font. These trials are referred to as “catch trials”. The scanner runs where the participant did not “catch” at least five out of seven trials were excluded from analyses. Participants with fewer than two out of three usable runs were excluded from the study. All included participants were right-handed, spoke fluent English, reported no known history of psychiatric or neurological disorders, and had normal or corrected to normal vision. The procedures of this study were approved by the Health Sciences Research Ethics Board for human subjects at the University of Western Ontario (See Appendix A and https://osf.io/ru4xb/).

3.2.2 Stimuli

Stimuli were created using MATLAB (Figure 3.1A). The code to create the stimuli is available on the OSF at (https://osf.io/9gfj4/). Habituation stimuli contained white ‘6’s in the font size 60 on a grey background (see Fig 3.1A for example of a habituation array). Participants were simultaneously adapted to three aspects of the array: the numerical symbol, the quantity, and the physical size of the digits. Deviant stimuli (i.e., stimuli that differed from the habituation stimuli in a particular way) were variations of an array of white Arabic digits randomly positioned on a grey background. Catch trials (i.e., trials for which participants were instructed to press a button) contained Arabic digits printed in blue on the same grey background. As previously stated, to meet our accuracy cut-offs, participants were required to “catch” at least 5 out of the 7 trials per run (Vogel et al., 2015). Multiple versions of the array for each condition were generated to ensure that participants did not learn the position of the Arabic digits within the array. E-prime 2.0 presentation software (Schneider, Eschman, & Zuccolotto, 2002) was used to project the stimuli onto a computer screen (resolution=800x600 pixels; colour bit depth = 16). The paradigm is available at (https://osf.io/gx63r/). The participants viewed the computer screen using a mirror system that was attached to the magnetic resonance imaging (MRI) head-coil.

3.2.3 Experimental Procedure

The fMR-A task was modelled after previous adaptation studies (Holloway et al., 2013; Vogel et al., 2015, 2017). Participants were instructed to attend to the screen and press a button when the digits on the screen turned blue (i.e., catch trials). The experiment included three fMR-A runs, each consisting of a stream of arrays of Arabic digits in Helvetica font punctuated by blank grey screens that were the same colour as the background of the arrays. The arrays were presented for 200 milliseconds and the blank grey screen for 1200 milliseconds (Figure 3.1A). During habituation, participants were presented with the digit '6' in four random locations of the screen in size 60 font between 5 and 9 times (average of 7 repeats). This allowed for a natural oversampling of the hemodynamic response function as the presentation of one trial (1400ms) was not synchronized with the scan repetition time (TR=1000ms). At jittered intervals (i.e., after 5-9 habituation trials), participants were presented with either a deviant trial (48 total trials across 6 conditions), a null trial (9 total), or a catch trial (7 total). In deviant trials, one aspect of the array of sixes was changed a small amount or a large amount. There were six conditions of deviant trial types (8 trials per deviant). Specifically, there were three types of deviants (symbolic, nonsymbolic, physical size), and each type changed a large amount or a small amount (small change, large change). In the symbolic condition, the numerical symbols changed from ‘6’s to '7's (small change), or to '2's (large change), while the quantity and physical size were held constant. In the nonsymbolic condition, the quantity changed from four to three (small change) or eight (large change) ‘6’s, but the symbol and physical size were held constant. For symbolic and nonsymbolic deviant conditions, the small change was a distance of 1 and the large change was a distance of 4. In the physical size condition, the size of the symbols decreased to font size 51 (small change) or increased to font size 86 (large change), but the symbol and quantity (i.e., four ‘6’s) remained unchanged. Critically, for the physical size condition, the area of the four digits was matched to the area taken up by the three digits in the quantity small change condition or the eight digits in the quantity large change condition. Specifically, the number of white pixels in the physical size condition was matched to the corresponding nonsymbolic deviant conditions using MATLAB. The code is available at (https://osf.io/rncv7/). In null trials, the participant was presented with another habituation trial array (i.e., four ‘6’s in size 60 font). In the catch trials, participants were presented with one of the 6 deviant trials, or a null trial in blue font. Participants pressed a button with the index finger of their right hand when the digits on the screen turned blue (i.e., catch trials). Catch trials were pseudo-randomly dispersed throughout each run. Participants had to push the button for at least five of the seven catch trials for the run to be included in the statistical analyses. See Figure 3.1B for an illustration of the adaptation, deviant, null, and catch trials.

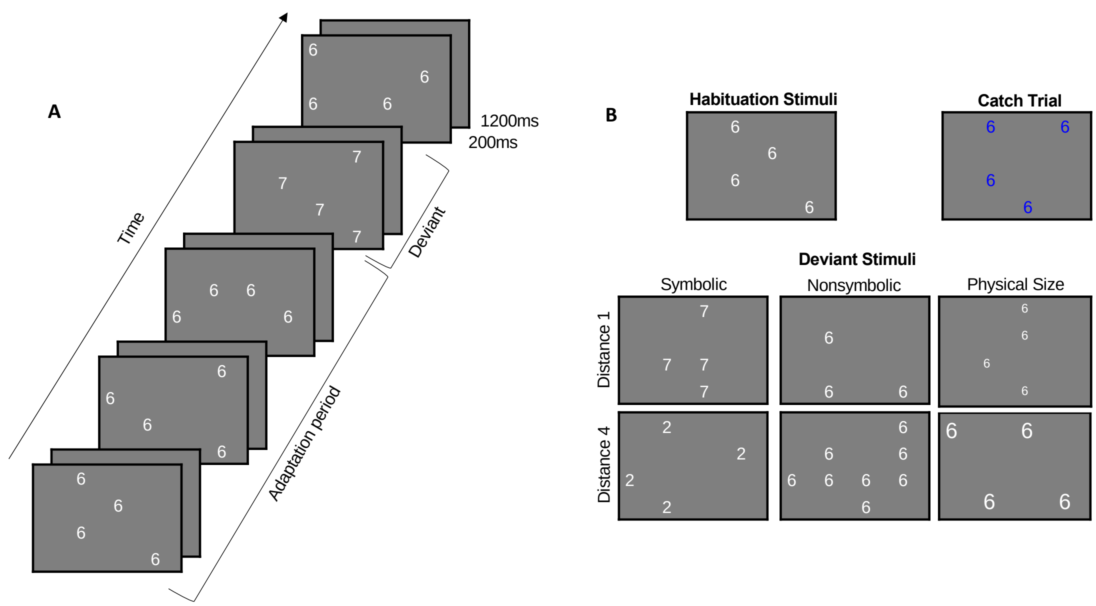

Figure 3.1 A) Example of the parallel adaptation paradigm: including the continuous presentation of the adapted stimulus (habituation period) followed by a deviant stimulus (in this case a symbolic deviant). B) Illustrations of examples of the adaptation stimulus, six deviant stimuli types (symbolic distance 1, symbolic distance 4, nonsymbolic distance 1, nonsymbolic distance 4, physical size small change, and physical size large change), and catch trial types (i.e., trials for which participants were instructed to press a button, to assure a minimum degree of attentiveness towards the stimuli presentation in the scanner).

3.2.4 fMRI Data Acquisition

Structural and functional images were acquired using a 3T Siemens Prisma Fit whole-body MRI scanner, using a 32-channel receive-only head-coil (Siemens, Erlangen Germany). A whole-brain high resolution T1-weighted anatomical scan was collected using an MPRAGE sequence with 192 slices, and a scan duration of 5 minutes and 21 seconds (isovoxel resolution = 1 × 1 × 1; TR = 2300 ms; TE 2.98 = ms; TI = 900 ms; FOV = 256 mm; flip angle = 9°). Functional MRI data were acquired using a blood oxygen level dependent (BOLD) sensitive T2* echo-planar (EPI) sequence. Forty-eight slices were acquired in a sequential multi-slice interleaved series with a multi-band accelerator factor of 4 (slice thickness = 2.5 mm; TR = 1000 ms; TE 30.00 = ms; FOV = 208 mm; flip angle = 40°). All data are publicly available at (https://openneuro.org/datasets/ds001848/versions/1.0.1).

3.2.5 fMRI Data Preprocessing

Structural and functional data were pre-processed and analyzed in Brain Voyager 20.6 (Brain Innovation, Maastricht, The Netherlands) using the software's preprocessing workflow (For workflow see: https://osf.io/3hr2g/). The structural brain data was extracted from the head tissue and intensity inhomogeneities were corrected to reduce the spatial intensity of the 3D volumes. Functional data were corrected for slice-scan time acquisition (cubic-spline interpolation algorithm), high-pass filtered (Fourier; cut off value of 2 sines/cosines cycles) and corrected for in-scanner head motion (Trilinear/sinc interpolation). A Gaussian smoothing kernel of 6-mm Full-Width-of-Half Maximum (FWHM) was applied to smooth the images. Structural and functional images were co-registered using a header-based initial alignment followed by a gradient-driven fine-tuning adjustment and normalized to MNI-152 space. A two gamma hemodynamic response function was used to model the expected bold signal (Friston, Josephs, Rees, & Turner, 1998). Baseline was calculated using the adaptation period as well as the between trial fixation periods. Catch trials were modelled as a predictor of no interest.

3.2.6 Data Analysis

3.2.6.1 Statistical Threshold

All of the statistical maps reported in the current study were first thresholded with an uncorrected p-value of .005. This statistical threshold was chosen based on reports from recent symbolic fMR-A studies (Vogel et al., 2015, 2017). The statistical whole-brain maps were corrected then for multiple comparisons at a statistical level of $p<.05$ using the cluster-level correction plugin in BrainVoyager (for review of this approach see Forman et al., 1995). The full width at half maximum (FWHM) in units of functional voxels (i.e., the smoothness) as well as the minimum cluster size ($p=.05$) based on the log-linear intra/extrapolation in millimeters (i.e., the cluster extent) are reported for each contrast with clusters of activation that reached a minimum threshold of $p < 0.005$, uncorrected and $p < 0.05$ cluster corrected at on whole-brain level.

3.2.6.2 Whole-brain Analyses

Whole-brain random-effects analyses were conducted using a general linear model (GLM) to examine overlapping and distinct BOLD responses to symbolic numerical magnitudes, nonsymbolic numerical magnitudes and the magnitude of physical size. All primary analyses were preregistered on the open science framework (OSF) (see https://osf.io/jrmpf/register/5771ca429ad5a1020de2872e for preregistration).

3.3 Results

3.3.1 Preplanned Analyses

3.3.1.1 Change Detection

Preliminary contrast analyses were run to examine what brain regions responded to changes in different stimulus dimensions. Regions that were associated with stimulus change detection were identified as regions associated with the change of one stimulus type (at both distances) over the change of the other two stimulus types (at both distances) (e.g., the symbolic change effect is calculated as [(symbolic distance 1 + symbolic distance 4) > (nonsymbolic distance 1 + nonsymbolic distance 4 + physical size distance 1 + physical size distance 4)]).

Results revealed that symbolic change detection (Cluster-Level: smoothing = 2.49; extent = 920 mm) was associated with activation in a widespread frontal-parietal-occipital network (Table 3.1, Figure 3.2). There were no brain regions that were activated above threshold in response to nonsymbolic change detection (Table 3.1, Figure 3.2). Physical size change detection (Cluster-Level: smoothing = 2.25; extent = 688 mm) was associated with activation in the right premotor cortex, right superior temporal gyrus, and left occipital region (Table 3.1, Figure 3.2). Critically, although these preliminary analyses highlight regions that are associated with the passive perception of change detection, these brain regions are not specifically associated with magnitude processing of symbols, quantities, and physical size.

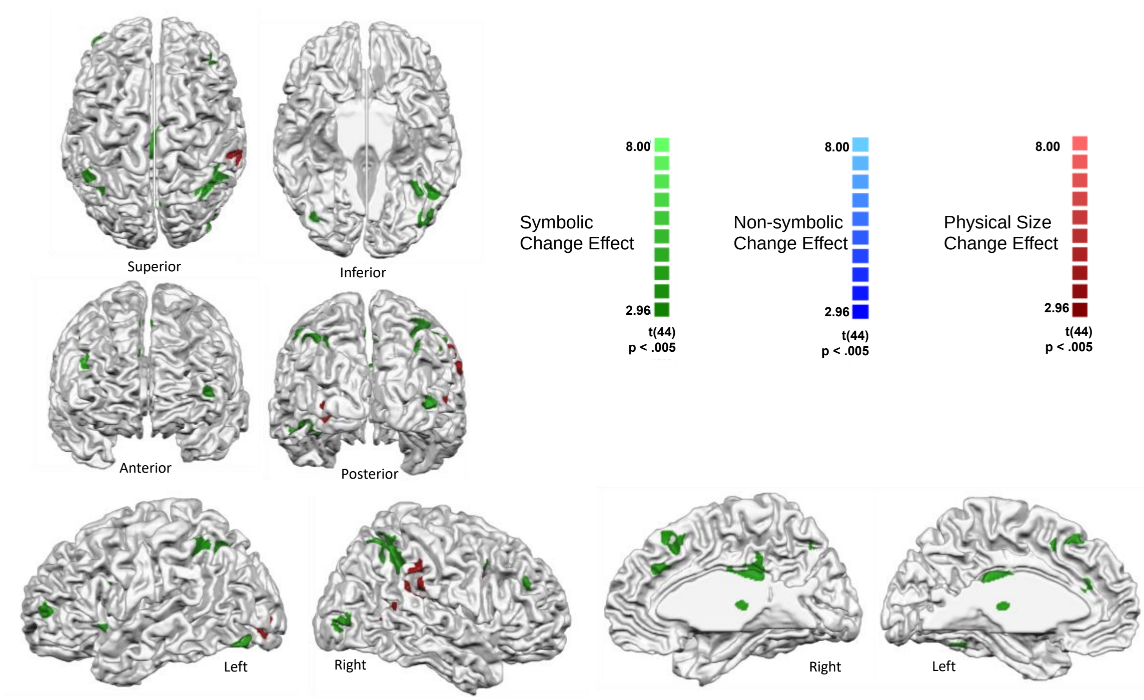

Figure 3.2 Change detection signal recovery from adaptation in the three deviant conditions (green = symbolic change detection, blue = nonsymbolic change detection, red = physical size change detection).

Table 3.1 Brain Regions Associated with Change Detection Signal Recovery from Adaptation

Hemi-sphere	Brain Region		Peak Coordinate			t	p	Cluster Size
	Juelich Histological Atlas	**Harvard-Oxford Structural Atlas**	**x**	**y**	**z**			(Number of Voxels)
		Symbolic Change Detection						
R	Anterior Intraparietal Sulcus	Superior Parietal Lobule, Angular Gyrus	33	-52	43	5.46	0.000002	9264
R		Frontal Pole, Middle Frontal Gyrus	42	38	25	3.70	0.0006	1286
R	Lateral Occipital Cortex	Visual Cortex	42	-88	-2	4.69	0.00003	1095
R	Thalamus	Corticospinal Tract	12	-10	4	4.80	0.00002	1563
R		Paracingulate Gyrus, Cingulate Gyrus	6	32	31	4.36	0.00008	2060
R	Callosal Body, Cingulum	Cingulate Gyrus	3	-34	28	4.46	0.00006	2754
R	Premotor Cortex	Superior Frontal Gyrus, Paracingulate Gyrus	0	26	52	4.37	0.00008	2573
L		Cerebellum	-6	-89	-32	4.45	0.00006	2322
L	Visual Cortex V4	Lateral Occipital Cortex, Occipital Fusiform Gyrus	-45	-76	-17	5.80	0.000001	6928
L	Anterior Intraparietal Sulcus,	Lateral Occipital Cortex, Superior Parietal Lobule, Angular Gyrus	-30	-61	46	4.44	0.00006	5670

	Superior Parietal Lobule							
L		Frontal Pole	-42	53	4	3.97	0.0003	1298
		Nonsymbolic Change Detection						
-	-	-	-	-	-	-	-	-
		Physical Size Change Detection						
R	Inferior Parietal Lobule	Supramarginal Gyrus	60	-37	22	4.46	0.00006	3008
R	Inferior Parietal Lobule	Angular Gyrus and Middle Temporal Gyrus	48	-49	13	4.27	0.0001	1098
L	Visual Cortex	Lateral Occipital Cortex, Occipital Pole	-30	-88	-2	4.51	0.00005	2538

3.3.1.2 Neural Distance Effects

We examined neural distance effects (i.e., distance 4>distance 1) to isolate brain regions associated with magnitude processing, of each deviant stimulus type (symbolic, nonsymbolic, physical size). To reveal neural correlates of the distance effects for each condition, we statistically compared distance four to distance one for the symbolic condition (symbolic distance 4 > symbolic distance 1), the nonsymbolic condition (nonsymbolic distance 4 > nonsymbolic distance 1) and the physical size condition (physical size large change > physical size small change). This analysis revealed that symbolic magnitude processing (Cluster-Level: smoothing = 2.10; extent = 571 mm) was associated with activation in the left inferior parietal lobule (Peak MNI Coordinate: -57, -64, 22; Cluster Size = 878 voxels) and the left orbitofrontal cortex (Peak MNI Coordinate: -36, 35, -14; Cluster Size = 944 voxels) (Figure 3.3A). Distinct from this, nonsymbolic magnitude processing (Cluster-Level: smoothing = 2.26; extent = 693 mm) was associated with activation in the right intraparietal sulcus (Peak MNI Coordinate: 27,

-67, 49; Cluster Size = 2381 voxels) (Figure 3.3B). Finally, physical size magnitude processing (Cluster-Level: smoothing = 2.45; extent = 836 mm) correlated with widespread activation spanning right parietal and occipital lobes (Peak MNI Coordinate: 42, -61, -11; Cluster Size = 25418 voxels), and a smaller region in the left occipital cortex (Peak MNI Coordinate: -45, -67, -11; Cluster Size = 5086 voxels) (Figure 3.3C). These results demonstrate that the processing of symbolic numerical magnitudes is left-lateralized, whereas the processing of nonsymbolic numerical magnitudes and physical size is right-lateralized. These data demonstrate that the brain regions that support symbolic and nonsymbolic number processing are potentially quite distinct. Furthermore, nonsymbolic numerical magnitude processing may actually be supported by brain regions used to process non-numerical magnitudes, such as physical size.

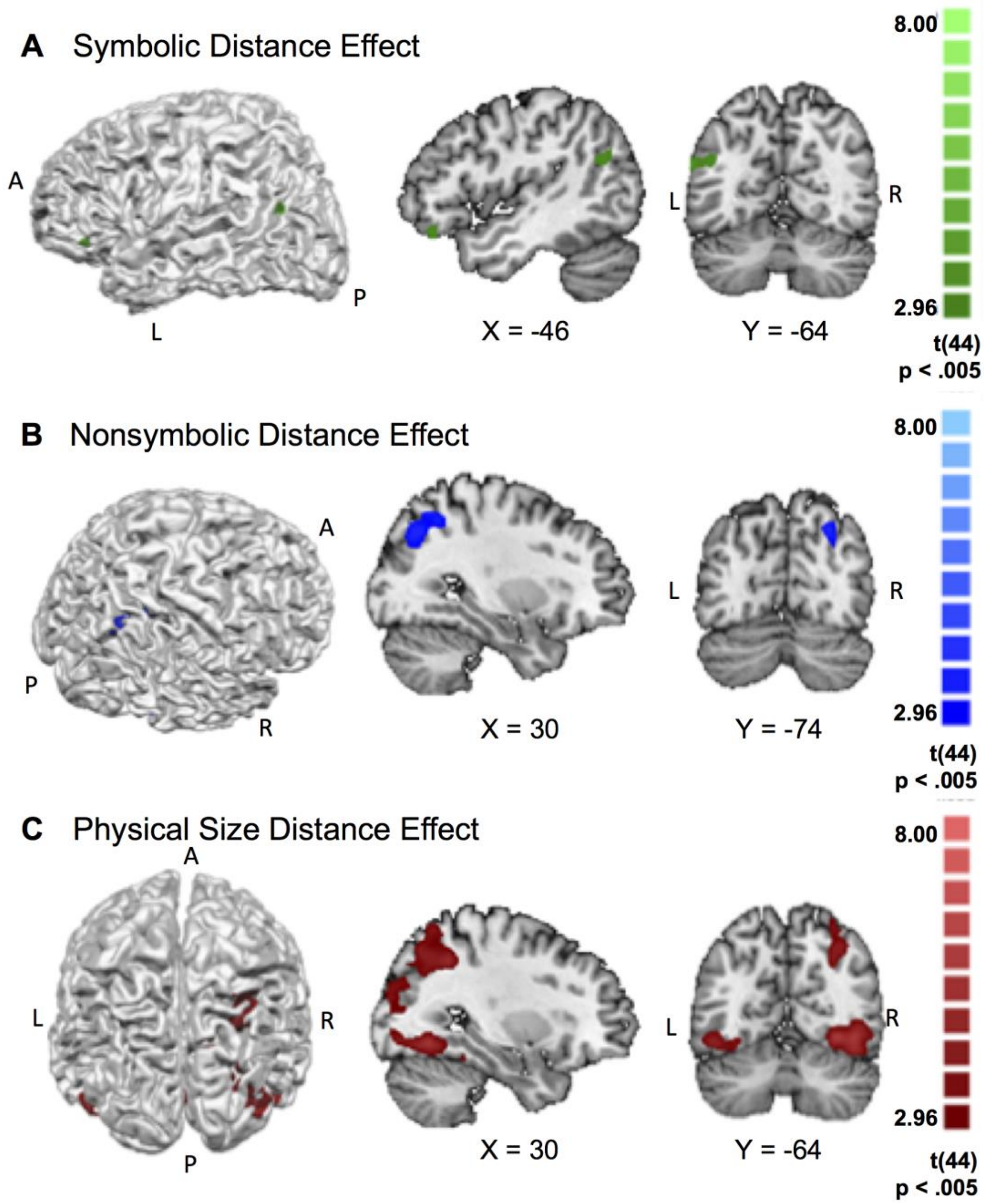

Figure 3.3 The neural rebound effects for: A) symbolic numerical magnitude processing defined as the degree of neural rebound for symbolic distance 4 deviant > symbolic distance 1 deviant, shown in green, B) nonsymbolic numerical magnitude processing, defined as the degree of neural rebound for nonsymbolic distance 4 deviant > nonsymbolic distance 1 deviant, shown in blue, C) physical size magnitude processing, defined as the degree of neural rebound for physical size large change deviant > physical size small change deviant, shown in red. This reveals that symbolic numerical

magnitudes are represented using distinct brain regions from those that support nonsymbolic and nonnumerical magnitude processing.

Following our pre-registered analysis plan, we next used a conjunction (∩) analysis to assess whether the brain regions associated with symbolic, nonsymbolic and physical size magnitude processing overlapped. This analysis [(Symbolic Distance 4 > Symbolic Distance 1) ∩ (Nonsymbolic Distance 4 > Nonsymbolic Distance 1) ∩ (Physical Size Large Change > Physical Size Small Change)] revealed that there are no brain regions commonly activated by symbolic, nonsymbolic and physical size magnitude processing.

To identify which brain regions support numerical magnitude processing specifically, the conjunction of the symbolic and nonsymbolic distance effects was contrasted against the physical size distance effect [((Symbolic Distance 4 > Symbolic Distance 1) ∩ (Nonsymbolic Distance 4 > Nonsymbolic Distance 1)) > (Physical Size Large Change > Physical Size Small Change)]. No brain regions that were significantly activated for numerical magnitude processing (symbolic and nonsymbolic) over and above brain regions associated with physical size processing were found.

The final set of preplanned analyses were included to identify whether the brain regions associated with symbolic, nonsymbolic and physical size magnitudes were format-specific. To do this, the neural distance effect of each format-specific magnitude was contrasted against the other two distance effects. The contrast examining symbolic specific activation [(Symbolic Distance 4 > Symbolic Distance 1) > ((Nonsymbolic Distance 4 > Nonsymbolic Distance 1) ∩ (Physical Size Large Change > Physical Size Small Change))] (Cluster-Level: smoothing = 2.21; extent = 654 mm) revealed that the left inferior parietal lobule supports symbolic magnitude processing over and above nonsymbolic and physical size (Peak MNI Coordinate: -57, -64, 22; Cluster Size = 1195 voxels) (Figure 3.4). In contrast, no brain region was specifically activated by nonsymbolic magnitude processing (i.e., the contrast [(Nonsymbolic Distance 4 > Nonsymbolic Distance 1) > ((Symbolic Distance 4 > Symbolic Distance 1) ∩ (Physical Size Large Change > Physical Size Small Change))]). The contrast examining which brain regions were specifically associated with physical size over and above numerical magnitude processing [(Physical Size Large Change > Physical Size Small Change) > ((Symbolic Distance 4 > Symbolic Distance 1) ∩ (Nonsymbolic Distance 4 > Nonsymbolic Distance 1))] (Cluster-Level: smoothing = 1.98; extent = 510 mm) implicated the right fusiform gyrus (Peak MNI Coordinate: 42, -67, -17; Cluster Size = 687 voxels). Together these analyses provide further evidence to support our key finding that the symbolic numerical magnitudes are processed using brain regions that are distinct from the regions that support the processing of nonsymbolic numerical magnitudes and physical size. In other words, the brain regions used to process culturally acquired symbols seem to be spatially distinct from the evolutionarily ancient systems that support nonsymbolic numerical magnitude processing and non-numerical magnitude processing, in human adults.

3.3.2 Post-Hoc Analyses

The findings from the pre-registered contrasts reveal that the neural correlates associated with the magnitude processing of symbolic numbers are spatially distinct from brain regions that support nonsymbolic and non-numerical magnitude processing. Critically, these pre-registered contrasts revealed that nonsymbolic magnitude processing and physical size magnitude processing both activated the right intraparietal sulcus, a region typically associated with number processing. Furthermore, although symbolic magnitude processing was specifically associated with activation in the left parietal lobe, no region in the parietal or frontal cortex was specifically activated by nonsymbolic or physical size processing. In view of this, a *post-hoc* conjunction analysis was run examining overlapping activation between nonsymbolic magnitude processing and physical size magnitude processing [(Nonsymbolic Distance 4 > Nonsymbolic Distance 1) ∩ (Physical Size Large Change > Physical Size Small Change)], (Cluster-Level: smoothing = 2.06; extent = 565 mm). Results revealed that one cluster in the right intraparietal sulcus was activated by the conjunction of nonsymbolic and physical size magnitude processing (Peak MNI Coordinate: 30, -67, 40; Cluster Size = 1412 voxels) (Figure 3.4). This post-hoc analysis suggests the right-lateralized parietal region is used to process *both* nonsymbolic and non-numerical magnitudes. Therefore, the brain regions that support nonsymbolic numerical magnitude processing may reflect a general magnitude system that processes both numerical and non-numerical, nonsymbolic information, rather than an abstract number processing system, that specifically supports the processing of numerical magnitudes.

To identify whether the brain region related to the conjunction of nonsymbolic and physical size processing was significant over and above symbolic number processing, the conjunction of the nonsymbolic and physical size distance effects was contrasted against the symbolic distance effect [(Nonsymbolic Distance 4 > Nonsymbolic Distance 1) $\cap$ (Physical Size Large Change > Physical Size Small Change) > (Symbolic Distance 4 > Symbolic Distance 1)]. There were no brain regions that were significantly activated for nonsymbolic numerical and non-numerical magnitude processing over and above brain regions supported by symbolic numerical magnitude processing. This post-hoc analysis indicates that while there is evidence that symbolic numerical magnitude processing is spatially distinct from nonsymbolic numerical magnitude processing and the processing of physical size, there is no strong spatial evidence for unique representations of nonsymbolic and physical size when contrasted to symbolic.

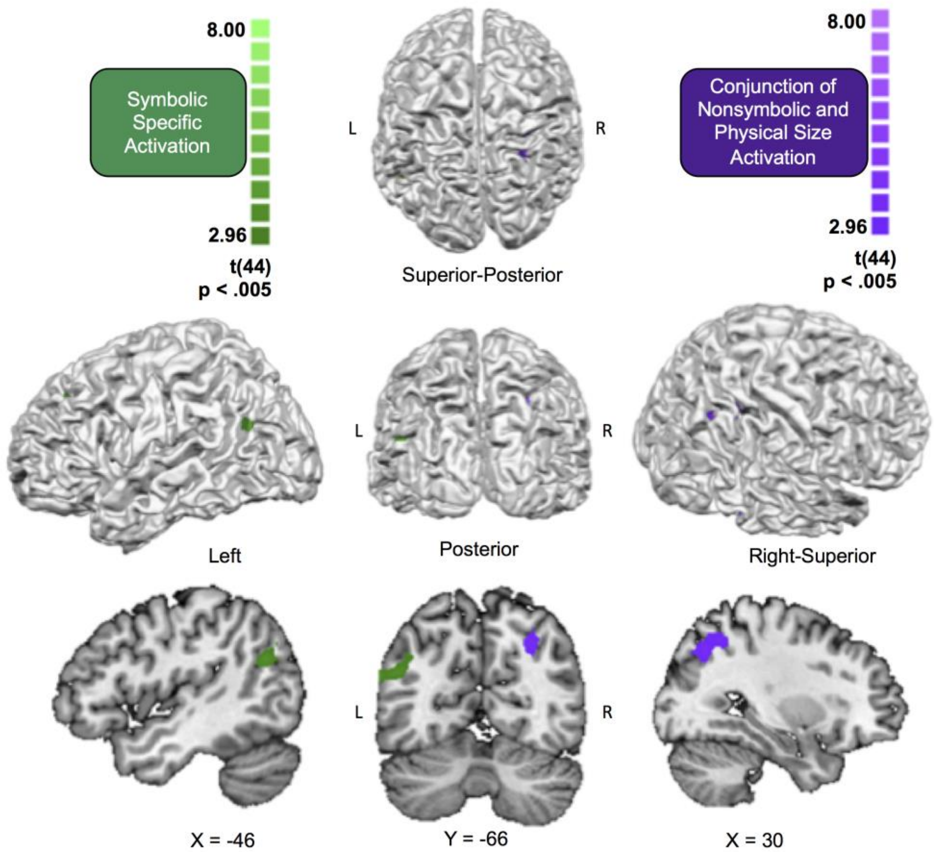

Figure 3.4 Symbolic specific rebound effect depicted in green. The conjunction between the rebound effects for nonsymbolic deviants and physical size deviants is depicted in purple.

Together, the preplanned combined with post-hoc univariate analyses indicate that nonsymbolic magnitudes are processed in the same brain region that is used to process physical size magnitude, namely the right intraparietal sulcus. In contrast, symbolic numerical magnitude processing is specifically associated with activation in the left inferior parietal lobule. However, though these univariate analyses suggest some spatial distinction between symbolic and nonsymbolic numerical magnitude processing, the conjunction of nonsymbolic and physical size processing was not significant over and above symbolic numerical magnitude processing. This suggests that while symbolic and nonsymbolic numerical magnitude processing seems to be lateralized in the parietal cortex both formats may still activate overlapping regions. Additionally, univariate analyses do not allow us to conclude that the underlying representations are unrelated. To address this outstanding issue, we used a multivariate approach to identify similarities and differences in the spatial patterns of neural activity for symbolic numerical magnitude processing, nonsymbolic numerical magnitude processing and the processing of physical size. More specifically, we used the multivariate method representational similarity analysis (RSA), to extract information about distributed patterns of representations within regions of interest in the brain. This method is valuable in advancing our understanding of similarities and differences in the underlying representations of symbolic, nonsymbolic and non-numerical magnitudes, rather than coarsely estimating spatial overlap.

3.3.2.1 Representational Similarity Analyses

We implemented RSA using Brain Voyager 20.6 (Brain Innovation, Maastricht, The Netherlands), to analyze the similarity between evoked fMRI responses for the symbolic distance effect, the nonsymbolic distance effect and the physical size distance effect in select regions-of-interest (ROIs). The ROIs were constructed by creating a sphere with a radius of 10mm around the weighted centre of the bilateral parietal clusters in the numerical passive viewing map from chapter 2 (Sokolowski, Fias, Mousa, & Ansari, 2017). The coordinates for the weighted centre of the parietal clusters are: 1) right hemisphere: MNI coordinates (x, y, z): 26, -55, 53) 2) left hemisphere: MNI coordinates (x, y, z): -28, -67, 43). For each ROI, a representational distance (or dissimilarity) matrix (RDM) was computed to assess the dissimilarity between the symbolic distance effect, the nonsymbolic distance effect, and the physical size distance effect (Figure 3.5). Note that the correlation calculated between patterns is a reflection of the similarity of the spatial patterns since this measure abstracts from the mean (and standard deviation) of the original values. The RDM contains a cell for each pair of experimental conditions. The colour of each cell represents a number that reflects the dissimilarities between the activity patterns associated with the two experimental conditions. Specifically, a Pearson correlation coefficient was calculated and subsequently transformed to a distance measure using the equation: $d = 1 – r$. These calculated d values, thus, range from 0.0 (minimum distance) to 2.0 (maximum distance) with value 1.0 in the middle representing no correlation. This data is further visualized using a multi-dimensional scaling (MDS) plot, which depicts the similarity between the conditions in a two-dimensional representation (Figure 3.5). Specifically, the conditions that are positioned closer together on the MDS plot have more similar neural activation patterns. Notably, results from this multivariate analysis revealed that nonsymbolic magnitude processing and physical size processing correlate more strongly at the multivariate level than either does with symbolic magnitude processing in both the right and the left hemispheres. Notably, this pattern of greater similarity between nonsymbolic and physical size compared to symbols is especially strong in the right hemisphere. In sum, these multivariate results revealed a dissimilar normalized pattern of activation for symbolic compared to nonsymbolic numerical magnitude processing in both the left and right parietal lobes. Together the converging evidence from the univariate and multivariate analyses show that, in the adult human brain, symbols are processed using distinct brain regions, and distinct patterns of activation, compared to nonsymbolic and non-numerical magnitudes.

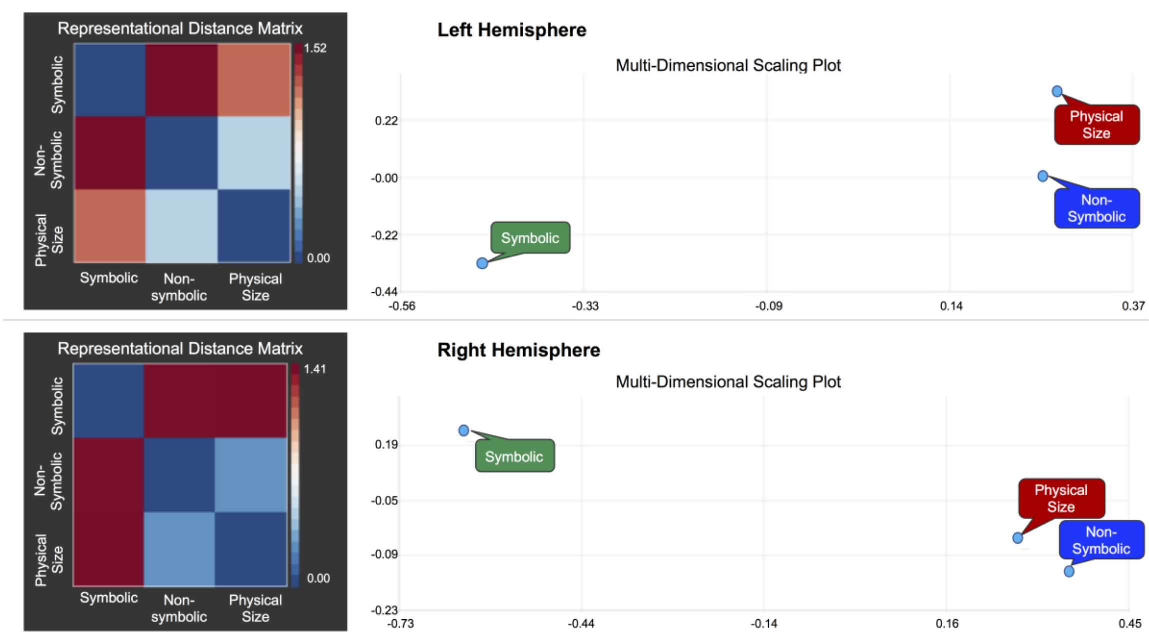

Figure 3.5 The left side of this figure illustrates the representational distance matrices (RDM) between the symbolic distance effect, the nonsymbolic distance effect, and the physical size distance effect in the left (top) and right (bottom) hemispheres. The numerical values that correspond to colours in the RDM refer to the distance measure

calculated using the equation: d = 1 – r. Therefore, the values can range from 0.0 (minimum distance) to 2.0 (maximum distance) with value 1.0 in the middle representing no correlation. The right side of this figure depicts the multi-dimensional scaling (MDS) plots, which are visualizations of the similarity between the three distance effects (symbolic, nonsymbolic, physical size) in two-dimensional space. The MDS plot is a visualization of the distances between conditions in a two-dimensional space that maximally satisfies the pairwise distances to all other conditions.

3.4 Discussion

The goal of the current study was to examine whether the uniquely human capacity to process symbolic numerical magnitudes relies on the same brain regions that support the processing of nonsymbolic numerical magnitudes (i.e., quantities). Parallel fMRI adaptation was developed and used to isolate and directly compare the semantic representations of symbols, quantities, and physical size while controlling for neural activation associated with other conditions, as well as inherent confounds of active tasks (Grill-Spector et al., 2006). Results revealed that the neural correlates of symbolic numerical magnitude processing are more distinct from nonsymbolic magnitude processing than has been assumed, at both the univariate and multivariate levels. At the univariate level, symbolic numerical magnitudes are represented in the left inferior parietal lobule, whereas both nonsymbolic numerical magnitudes and non-numerical magnitudes (i.e., physical size) are represented in the right intraparietal sulcus. These findings align with previous research indicating that different number formats (symbolic and nonsymbolic) are lateralized within the parietal cortex (For review see: Sokolowski & Ansari, 2016). Specifically, activation in the left parietal lobule is specific to symbolic number processing, whereas the right parietal lobule is more activated during nonsymbolic magnitude processing (Sokolowski, Fias, Mousa, et al., 2017). At the multivariate level, normalized patterns of activation for symbolic numerical magnitude processing in both the left and right parietal lobes were different compared to patterns of activation for nonsymbolic magnitude processing; this also converges with previous research (Bulthé et al., 2014; Eger et al., 2009; Lyons et al., 2014). This suggests that in the adult human brain, symbolic numerical magnitudes are processed in a way that is spatially and representationally distinct from the processing of nonsymbolic numerical magnitudes.

The findings from the current study suggest that adult humans possess two distinct systems to support magnitudes: 1) a symbolic system used specifically to represent symbolic numerical magnitudes, and 2) a general magnitude system used to represent both discrete and continuous magnitudes. These findings directly contrast the findings from Chapter 2 of this thesis, as well as the predominant view in the field of numerical cognition, namely that symbolic and nonsymbolic numbers are processed using *both* overlapping as well as distinct neural mechanisms (For review see: Cohen Kadosh, 2008; Sokolowski, Fias, Mousa, et al., 2017; Sokolowski & Ansari, 2016). The parallel adaptation paradigm developed and employed in the present study overcomes major confounds of previous research that use active tasks such as decision making, and motor processing for these active tasks (Grill-Spector et al., 2006). Indeed, previously reported overlapping activation during the processing of symbolic and nonsymbolic numerical magnitudes likely resulted from overlapping task demands, or the effortful process of mapping symbols onto quantities in the case of cross-format designs. Using our parallel adaptation approach, we discovered that the underlying brain regions supporting symbolic number processing are quite distinct from the regions that correlate with processing nonsymbolic magnitude processing in human adults.

Results from the current study also show that the neural representations of nonsymbolic numerical magnitudes are nearly indistinguishable from the neural correlates that support the processing of non-numerical magnitudes, specifically physical size. This aligns with the growing body of research highlighting that nonsymbolic numbers are inherently confounded by non-numerical magnitudes, such as physical size (Leibovich & Henik, 2013). Additionally, our finding that nonsymbolic numerical magnitudes and non-numerical magnitudes are supported by the same neural substrates directly contradicts the dominant view in numerical cognition, that symbolic and nonsymbolic numerical magnitudes are supported using an abstract number processing system that is specifically attuned to the processing of discrete quantities (Brannon, 2006; Cantlon, 2012; Dehaene et al., 1998, 2003; Nieder & Dehaene, 2009). Our findings also show that the system used to process nonsymbolic numbers may, in fact, be part of a general magnitude processing system used to process both discrete as well as continuous magnitudes (Cohen Kadosh et al., 2008; Lyons et al., 2012, 2014; Sokolowski, Fias, Bosah Ononye, et al., 2017; Walsh, 2003).

A key finding from our study, that symbols are processed using different brain regions and produce different patterns of activation compared to nonsymbolic and non-numerical magnitudes, highlights the need to consider what is actually special about symbols. One key way in which symbols differ from the quantities that they represent is that symbols are processed exactly rather than approximately, regardless of magnitude (Hyde, 2011; Negen & Sarnecka, 2015; Núñez, 2017; Pica, Lemer, Izard, & Dehaene, 2004). This means that to understand the meaning of a large symbolic number, an adult does not need to map that symbol onto a pre-existing representation for the corresponding nonsymbolic numerical magnitude. Instead, learning counting principles that underlie symbolic numbers is a sufficient condition for understanding any symbolic number (Gallistel & Gelman, 1992; Gelman & Gallistel, 1978; Le Corre & Carey, 2014). The idea that symbols can be represented exactly, whereas nonsymbolic and non-numerical magnitudes can only be processed approximately, provides a potential explanation for why the passive processing of symbolic and nonsymbolic numerical magnitudes are associated with separate brain regions.

The multivariate results of this study provide very clear evidence for representational dissimilarity between symbolic numerical magnitude processing compared to nonsymbolic and non-numerical magnitude processing. However, the univariate results indicate that the neural correlates of symbolic number processing are spatially distinct, but the brain region associated with the conjunction between nonsymbolic and non-numerical magnitude processing is not significantly activated over and above symbolic numerical magnitude processing. This suggests that although there is evidence that symbolic number processing is spatially distinct from nonsymbolic and non-numerical magnitude processing, there is no strong spatial evidence for unique representations of nonsymbolic and physical size. In other words, the brain region that supports nonsymbolic and non-numerical magnitude processing is also at least partially activated by symbolic number processing. Therefore, the data from the current study provides some evidence that the brain regions that are activated during the passive processing of nonsymbolic and non-numerical magnitudes are also activated by symbolic numerical magnitudes. However, the neural correlates the support the uniquely human, culturally acquired, ability to represent numbers symbolically is supported by a set of brain regions that is quite distinct from the brain regions that support nonsymbolic numerical magnitude processing and non-numerical magnitude processing.

3.4.1 Limitations

There are several important limitations to the current study. First, as the stimuli consist of arrays that include both symbolic and nonsymbolic numerical magnitudes, the possibility that these different formats automatically influence each other during processing (e.g., Morton, 1969; Naparstek & Henik, 2010; Pansky & Algom, 2002) cannot be ruled out. However, the fact that a neural distance effect was found for both symbolic and nonsymbolic deviants, in distinct brain regions, suggests that the paradigm captured elements of magnitude processing that were specific to each format. In chapter 4, of the current thesis, I address this question by empirically evaluating the automatic influence of symbols and quantities on each other at the behavioural level. A second limitation of the current study is that, due to attentional time constraints of the participants, it was not possible to include multiple numerical values for the habituation stimulus and within deviant categories. In other words, only one symbolic and nonsymbolic numerical magnitude was included for the habituation array and each change condition. In view of this, the results from this study are specific to the particular magnitudes we included and should not be generalized to all numerical magnitudes. Future research is needed to examine whether these effects hold across multiple different symbols and quantities for both habituation and deviant stimuli.

3.4.2 Conclusions

This study provides evidence in support of the notion that the human adult brain processes symbolic numerical magnitudes and nonsymbolic numerical magnitudes using regions that are more distinct than has been assumed. Indeed, these findings directly conflict with the dominant view in the field that symbolic and nonsymbolic numerical magnitudes are supported by a single abstract number processing system (Cantlon, 2012; Dehaene, 2007; Dehaene et al., 1998; Nieder & Dehaene, 2009). Instead, data from the current study suggest that in human adults, culturally acquired symbolic representations and evolutionarily ancient nonsymbolic representations may be represented by two distinct systems. Our data highlight the need for the field of numerical cognition to move away conducting research with the goal of canvassing the brain in search of an abstract number processing system. Instead, efforts should be shifted towards uncovering the multifaceted behavioural and neural consequences of learning the complex, uniquely human skill of symbolic abstraction.

3.5 References

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Chapter 4

4 Number Symbols are Processed More Automatically than Nonsymbolic Numerical Magnitudes: Findings from a Symbolic-Nonsymbolic Stroop Task

4.1 Introduction

Basic number processing is a cognitive foundation that supports mathematical thinking. Basic number processing is defined as the ability to understand, estimate, and/or discriminate between numerical magnitudes. From very early in development humans have the ability to process nonsymbolic numerical magnitudes (often referred to as quantities) (e.g.,'●●●' vs. '●●') (Brannon, 2006). This capacity to process nonsymbolic numerical magnitudes is shared with non-human primates as well as other species (For reviews see: Cantlon, 2012; Dehaene, 2007). This suggests that the ability to process nonsymbolic numerical magnitudes has a long evolutionary history. Critically, unlike non-human species and infants, human adults, in cultures that teach math symbolically, have the unique, culturally acquired ability to process numbers symbolically (e.g.,'3').

The dominant assumption in the field of numerical cognition has been that this culturally acquired ability to represent numbers symbolically is linked to an evolutionarily ancient system used to process nonsymbolic numerical magnitudes (Brannon, 2006; Dehaene, 2007; Dehaene, Piazza, Pinel, & Cohen, 2003; Halberda, Mazzocco, & Feigenson, 2008; Nieder & Dehaene, 2009). However, a growing body of research, including data from Chapter 2 and 3 of this thesis, has revealed that symbolic and nonsymbolic numerical magnitudes are processed more distinctly than has been assumed (Cohen Kadosh et al., 2011; Cohen Kadosh, Kaas, Henik, & Goebel, 2007; Cohen Kadosh & Walsh, 2009; De Smedt et al., 2013; Holloway et al., 2010; Lyons, Ansari, Beilock, 2012; Sokolowski et al., 2016). Previous research has used *effortful* number processing tasks (e.g., Ansari, 2008; Dehaene, Dehaene-Lambertz, & Cohen, 1998; Fias, Lammertyn, Reynvoet, Dupont, & Orban, 2003; Fulbright, Manson, Skudlarski, Lacadie, & Gore, 2003; Holloway & Ansari, 2008, 2009; Moyer & Landauer, 1967) and *automatic* number processing tasks (e.g., Furman & Rubinsten, 2012; Naparstek & Henik, 2010, 2012;

Naparstek, Safadi, Lichtenstein-Vidne, & Henik, 2015; Pansky & Algom, 2002; Pavese & Umiltà, 1998, 1999; Windes, 1968) to attempt to unravel how human adults process symbols and quantities. Effortful processing tasks require participants to actively attend to the presented stimuli and typically, make a decision based on these stimuli. For example, a number comparison task where participants are presented with two numerical magnitudes and asked to indicate which of the two numerical magnitudes has more items is an example of an effortful number processing task (e.g., Buckley & Gillman, 1974; Holloway & Ansari, 2009; Moyer & Landauer, 1967). Automatic processing refers to information processing that occurs in situations where the information is not task-relevant. An example of an automatic number processing task is the Numerical Stroop Task. In a Numerical Stroop Task a participant is presented with two digits that differ both in numerical magnitude and in physical size (e.g., 3 and 4) and are asked to indicate which digit is numerically or physically larger (Henik & Tzelgov, 1982; Leibovich, Diesendruck, Rubinsten, & Henik, 2013). When participants complete this task a so-called size congruity effect (SCE) is obtained. The SCE reflects the finding that the dimension to which the participant does not need to attend automatically influences speed and accuracy on the comparison task. For example, when making a physical size judgment, on a Numerical Stroop task that includes two different Arabic numerals in different size fonts, the numerical magnitude of the symbols being compared automatically influences judgments of the physical size. This finding, that the semantic meaning of a symbols affects physical size judgments, despite the fact that the participants do not need to process the semantic meaning of the number to succeed at the task, has been taken to suggest that the system used to process the physical size of an Arabic numeral is overlapping with the system used to process the semantic meaning of the Arabic numeral. Critically, although this task is useful in revealing the way humans automatically process symbolic numerical magnitudes in relation to the non-numerical magnitude, physical size, this paradigm cannot be used to address questions pertaining to the difference and similarities in processing symbolic and nonsymbolic numerical magnitudes.

An important way to advance our understanding of how (or whether) symbolic and nonsymbolic numerical magnitudes are connected is to study the degree to which one automatically influences the other during processing. Currently, there is a limited understanding of the connection between symbolic and nonsymbolic numerical magnitudes at different levels of processing. An automatic processing (i.e., Stroop-like) task is an ideal way to explore the link between symbolic and nonsymbolic numerical magnitudes. If symbols and quantities are processed using the same system, then they should automatically activate each other, but if they are not closely connected then the processing of one format (i.e., symbol or quantity) should not activate or influence the processing of the other format. Notably, in line with research suggesting that symbols and quantities are not as connected as has been assumed (including chapter 2 and 3 from the current thesis and reviewed here: Cohen Kadosh & Walsh, 2009; Sokolowski & Ansari, 2016), it is possible that there will be an asymmetry in activation, namely that only one of the formats will automatically activate the other. Despite years of research, the question of whether symbolic (i.e., Arabic digits) and nonsymbolic numerical magnitudes (i.e., quantities) influence each other in the same or an asymmetrical way has not been examined. The current study will identify whether symbols and quantities are processed similarly during effortful and automatic, processing.

Amongst the most frequently cited evidence to support the notion that symbols are fundamentally linked to nonsymbolic numerical magnitudes is the finding that human adults produce a ‘distance effect’ when making comparative judgements of both symbolic and nonsymbolic numerical magnitudes (e.g., Dehaene, Dehaene-Lambertz, & Cohen, 1998; Holloway & Ansari, 2008, 2009; Krajcsi, Lengyel, & Kojouharova, 2016; Moyer & Landauer, 1967; Pavese & Umiltà, 1998; van Opstal & Verguts, 2011). The distance effect is the highly replicable finding that humans are faster and more accurate at judging which of two numerical magnitudes is numerically greater when those magnitudes are numerically close together, rather than far apart. There have been many reports of similar distance effects during the processing of symbolic and nonsymbolic numerical magnitudes that have been replicated across many studies (Buckley & Gillman, 1974; Holloway & Ansari, 2008; Holloway, Price, & Ansari, 2010; Krajcsi, Lengyel, & Kojouharova, 2016; Moyer & Landauer, 1967) and taken as evidence that symbolic and nonsymbolic numerical magnitudes are represented using a shared analogue magnitude system (Dehaene, 2007; Dehaene et al., 1998). Numerical distance has been shown to affect effortful (Buckley & Gillman, 1974; Holloway & Ansari, 2009; Moyer & Landauer, 1967) as well as the automatic processing of symbols and quantities (Henik & Tzelgov, 1982; Pavese & Umiltà, 1998, 1999). The finding that numerical distance influences automatic processing of numerical magnitudes has been taken to suggest that the presence of a numerical distance effect is a general property of activating a numerical magnitude, rather than a consequence of attention when processing magnitudes. More generally, the effect of numerical distance has been used to assess the degree to which the underlying representations that support the processing of numerical magnitudes are overlapping and thus have been interpreted to be a measure of representational precision (Nieder & Dehaene, 2009; Verguts & Fias, 2004). Therefore, assessing the whether the influence of symbols and quantities on each other is modulated by numerical distance will add to the current understanding of the connection between symbols and quantities by identifying not only whether symbols and quantities are processed in parallel, but also whether the representational precision of this influence is symmetrical. In other words, we will explore whether numerical distance influences symbols and quantities differently during effortful and automatic processing to understand whether the representational structures supporting symbolic and nonsymbolic numerical magnitude processing are the same or distinct.

In the current study, we assess whether symbolic and nonsymbolic numerical magnitudes are processed similarly by examining whether the processing of one format activates the processing of the other format. We will conclude that symbols and quantities are processed in parallel if the automatic processing of both symbols and quantities do indeed influence the effortful processing each other. Additionally, we will conclude that symbolic and nonsymbolic numerical magnitudes are processed using the same representational structure if the automatic influence of symbols and quantities on each other are modulated by numerical distance in the same way. However, finding that symbols and nonsymbolic numerical magnitudes do not influence each other will be taken to suggest that symbols and quantities are processed by distinct systems. Moreover, the finding of an asymmetry between the processing of symbols and quantities, namely that only one of the two dimensions automatically influences the other, or that the automatic influence of symbols and quantities are differentially modulated by numerical distance will be taken as support for the idea that similar but ultimately distinct representational systems support the processing of symbols and quantities. In the following experiments, we examine the effortful and automatic processing of symbolic and nonsymbolic numerical magnitudes (i.e., symbols vs. quantities). Additionally, we examine how numerical distance influences the effortful and automatic processing of symbols compared to quantities. This study will reveal whether there is an asymmetry in the automaticity of the processing magnitudes of different number formats.

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4.2 Experiment 1

4.2.1 Experiment 1: Introduction

In the current study, we adapt the famous colour Stroop paradigm (Stroop, 1935), to measure both the effortful and automatic processing of symbolic and nonsymbolic numerical magnitudes within the same task. Stroop paradigms have been widely used in psychology to examine the degree to which an irrelevant stimulus influences the processing of a relevant stimulus. The original Stroop effect revealed that participants are slower and less accurate at naming a font colour of a printed word if the meaning of the word and font colour conflict (Stroop, 1935). For example, participants were slower and less accurate at identifying that the font colour of a word if the font colour is different from the semantic meaning of the printed word (i.e., red).

Previous research studies have used Stroop-like tasks to assess the automatic processing of symbolic numbers (Henik & Tzelgov, 1982; Naparstek et al., 2015; Pansky & Algom, 2002). As discussed above, the Numerical Stroop Task, a task that requires participants to judge which of two digits (e.g., 3 vs 5) was larger either in physical size or in numerical magnitude, is the most widely used assessment of the automatic processing of symbolic numerical magnitudes (Henik & Tzelgov, 1982). Results revealed that judgments of physical size were faster than judgments of symbolic magnitude, suggesting that participants are more efficient at effortfully processing size compared to the numerical magnitude represented symbolically. However, physical size judgments were affected by the numerical magnitude of the digit. Moreover, the degree to which the numerical magnitude of the symbol influenced the processing of the physical size was associated with numerical distance. Specifically, physical size judgments were more influenced by Arabic numeral pairs with relatively larger numerical distances. Therefore, in the same way that larger numerical magnitude is more obvious when comparing two magnitudes with a large numerical distance, larger numerical distances between two irrelevant numerical magnitudes make the automatic influence of the irrelevant dimension more salient. This indicates that numerical distance is automatically processed even when it is irrelevant to form the judgment of which of two symbols is physically larger. This finding, that numerical distance of the symbols is automatically computed during the effortful processing of physical size, has been taken to suggest that physical size and semantic meaning of the numerals are processed in parallel. Other research that has examined the automatic processing of symbols and quantities presented participants with a single array containing a quantity of symbolic digits (e.g., a single array containing six of the Arabic digit ‘7’). Participants were instructed to compare either the symbolic or nonsymbolic numerical magnitude in the array to the number five (comparison task), or to indicate if the numerical quantity was an even or odd number (parity task) (Naparstek & Henik, 2010). Results revealed that symbols influenced the processing of quantities for both the comparison and parity tasks, whereas quantities only influenced the processing of symbols on the comparison task. This suggests that symbols may be processed more automatically than quantities. Critically, Naparstek and colleagues included a single array of symbols (e.g., six of the symbol ‘7’), and asked participants to compare either the symbol or the quantity to the number five. Therefore, in these tasks, both symbols and quantities were being compared to a symbolic referent held in mind. Consequently, it is possible that the asymmetry between the symbolic and nonsymbolic numerical magnitudes is due to the fact that, for the nonsymbolic task, the participants were comparing between formats (i.e., nonsymbolic to symbolic), whereas in the symbolic task, participants were comparing a symbol to a symbolic referent. Consequently, in the current study, we create a Symbolic-Nonsymbolic Stroop paradigm which allows us to examine how symbols and quantities influence each other, without requiring a transformation between formats, and also assess whether the influence of symbols and quantities on each other is symmetrically modulated by numerical distance. Findings from the current study will illuminate whether the influence of symbols and quantities on each other is symmetrical and will, therefore, allow us to identify whether symbols and quantities processed separately or in parallel, and with the similar to distinct representational precision. These findings are important to identify whether symbols are processed using the ancient system that evolved to process nonsymbolic numerical magnitudes, or if symbols are supported by a similar but ultimately distinct representational system.

4.2.1.1 The Symbolic-Nonsymbolic Stroop Paradigm

In the current study, we examined whether the effortful and automatic processing of symbolic numerical magnitudes (e.g., 3) is distinct from effortful and automatic processing of the nonsymbolic numerical magnitudes they represent (e.g., •••) using a Symbolic-Nonsymbolic Stroop paradigm. Critically, the stimuli in this paradigm consisted of two quantities of symbols (e.g., 3333 vs. 444). The inclusion of two sets of symbols and quantities in all stimuli meant that we were able to not only assess effortful and automatic processing of symbols and quantities independently but also the influence that symbols and quantities have on each other. During this paradigm, participants were asked to compare adjacent arrays of number symbols (e.g., 4444 vs 333) and indicate the side containing *either* the greater quantity of symbols (nonsymbolic task) or the side containing the numerically larger symbol (symbolic task). This means that symbolic and nonsymbolic numerical magnitude acted as *both* the relevant dimension (i.e., the dimension that the participant was instructed to attend to) and the irrelevant dimension (i.e., the dimension that the participant needed to ignore). There were congruent trials, where the larger symbolic and nonsymbolic numerical magnitude appeared on the same side of the screen (e.g., 333 vs. 4444), incongruent trials, where the larger symbolic and nonsymbolic numerical magnitude appeared on opposite sides of the screen (e.g., 3333 vs. 444), and neutral trials, where the irrelevant dimension was the same across both sides of the screen (e.g., 3333 vs. 333 for nonsymbolic; 333 vs. 444 for symbolic). In this task, the numerical distance between the numerical magnitudes being compared was systematically varied across trials. The use of the Symbolic-Nonsymbolic Stroop paradigm is optimal to test the following predictions and ultimately assess whether symbolic numerical magnitudes are processed in the same way as the nonsymbolic numerical magnitudes under different attentional conditions.

We anticipate several possible outcomes for the effortful and automatic processing of symbols compared to quantities. The first of these is that symbolic and nonsymbolic numerical magnitudes will be processed in the same way both effortfully and automatically. Specifically, this would mean that no difference will be observed in participants ability to compare symbols and quantities, and symbols and quantities will automatically influence each other in the same way. This idea is supported by research suggesting that symbolic and nonsymbolic numerical magnitudes are processed by the same analogue magnitude processing system (e.g., Cantlon et al., 2009; Dehaene, 2007; Dehaene et al., 1998; Nieder & Dehaene, 2009; Piazza et al., 2007). In view of research that reports an asymmetry of the processing of symbolic and nonsymbolic numerical magnitudes, including chapter 2 and 3 of the current thesis, (Krajcsi et al., 2016; Krajcsi, Lengyel, & Kojouharova, 2018; Lyons et al., 2012; Lyons, Nuerk, & Ansari, 2015; Sokolowski, Fias, Mousa, & Ansari, 2017; Vogel, Grabner, Schneider, Siegler, & Ansari, 2013) we also predict a second possible outcome. The second possible outcome is that results will reveal an asymmetry in the processing of symbols and quantities either during effortful processing, automatic processing, or both. For this potential outcome, we predict that symbols will be processed more efficiently than quantities during effortful processing and automatic processing. This prediction runs in contrast to the finding that symbols are processed less automatically than physical size (Henik & Tzelgov, 1982). However, we argue that enumerating a large set of discrete objects (rather than focussing on the size of a single object) requires a greater degree of processing, and therefore will be less efficient and less automatic. In view of this, we also predict that if there is an asymmetry between the processing of symbolic and nonsymbolic numerical magnitudes it will be due to the fact that symbols influence the processing of quantities more than quantities will influence the processing of symbols. Finally, based on research reporting an asymmetry in the distance effects of symbolic and nonsymbolic numerical magnitudes (Buckley & Gillman, 1974; Furman & Rubinsten, 2012; Holloway et al., 2010; Moyer & Landauer, 1967; Rubinsten, Henik, Berger, & Shahar-Shalev, 2002) we predict that the effortful processing of quantities will produce a larger distance effect than the effortful processing of symbols. In summary, this study uses a novel task to compare the effortful and automatic processing of symbolic and nonsymbolic numerical magnitudes.

4.2.2 Experiment 1: Method

4.2.2.1 Participants

Eighty healthy adult participants (M_{age}=21.4, SD_{age}=3.01; 31 males, 49 females) were recruited at the University of Western Ontario in London, Ontario. Participants provided written consent before participating in the study. The session took approximately two hours and participants were compensated $5 CAD per half-hour (average $20 CAD total). All procedures were approved by the University of Western Ontario Non-medical Research Ethics Board (See Appendix A).

4.2.2.2 Materials

4.2.2.2.1 Symbolic-Nonsymbolic Stroop Task.

Each participant performed two kinds of magnitude comparisons on the same set of stimuli. Stimuli were composed of two arrays of Arabic numerals (numbers 1 to 9) in a four by four array (see Fig 1). An array contained a certain quantity of Arabic numerals (e.g., six “6’s). The remaining spaces in the array were filled with the star symbol (*) as has been done in previous research (Naparstek et al., 2015; Pansky & Algom, 2002), to control for continuous properties such as area (Leibovich & Henik, 2013). Specifically, including ‘*’ in all spaces that did not contain a symbol allowed us to keep the total area of the numerical displays constant throughout all trials. Although this does not remove all associations between continuous properties and quantities (i.e., the proportion of spots filled by digits still changes based on quantity) it does control for salient continuous magnitudes that have been reported to significantly influence the processing of nonsymbolic numerical magnitudes, such as area, density, and convex hull (For review see: Henik, Gliksman, Kallai, & Leibovich, 2017; Henik, Leibovich, Naparstek, Diesendruck, & Rubinsten, 2011; Leibovich & Henik, 2013; Leibovich, Katzin, Harel, & Henik, 2016). Twenty different versions of each array were generated using MATLAB to ensure that participants did not learn the position of the Arabic digits within the arrays. See figure 4.1 for an example of two arrays. The stimuli were presented using

OpenSesame (Mathôt, Schreij, & Theeuwes, 2012), with a resolution of 800 x 600. The stimuli, code to create the stimuli, and the OpenSesame experiments (which include trial lists), are publicly available at on the Open Science Framework (OSF) at https://osf.io/qyczk/.

Figure 4.1 An example of two arrays presented to participants the contain quantities of Arabic numerals. The array on the left contains six of the Arabic numeral '6', and the array on the right contains two of the Arabic numeral '2'.

The participant performed both a symbolic comparison task and a nonsymbolic comparison task on all pairs of arrays. In the **symbolic task**, the participant had to indicate which array contained the numerical symbol with the larger magnitude. In the **nonsymbolic task**, the participant had to indicate which array contained the greater quantity of numerical symbols (five '3's vs. two '2's). In the congruent condition, the larger symbol and the greater quantity appeared on the same side of the screen. In the incongruent condition, the side with larger symbol appeared opposite to the side with the greater quantity. Importantly, the participant was presented with the same set of stimuli for the symbolic task and the nonsymbolic task for both the congruent and incongruent conditions. In the neutral condition, the irrelevant dimension was the same across both sides of the screen and depended on the condition. In the symbolic neutral condition, the two arrays contained different symbolic numbers, but the quantity of symbolic numbers was held constant between the stimuli and matched one of the two symbolic numbers. In the nonsymbolic neutral condition, the quantity of the symbolic numbers in the two arrays was different, but both arrays contained the same symbolic numbers that were the same as one of the two quantities. In the congruent and incongruent conditions, the distance between the relevant dimension (i.e., what the participant is told to compare) and the irrelevant dimension (i.e., what the participant must ignore) was the same and ranged from 1-6, with 12 trials per distance. The distance between the relevant dimension in neutral condition was matched to the congruent and incongruent conditions, and the irrelevant dimension in the neutral condition was always 0. See Figure 4.2 for examples of stimuli for congruent, incongruent, and neutral conditions for both the symbolic and nonsymbolic comparison task.

Participants were randomly presented with two blocks of 216 trials (432 total trials) on the symbolic task and on the nonsymbolic task. Of the 216 trials, 72 stimulus pairs were congruent, 72 were incongruent, and the remaining 72 trials were neutral. Each of the 72 trials consisted of 12 trials at each of distance 1-6. Notably, only 108 of the 216 trials had unique number pairs. The other 108 trials had the same numbers as the original 108 trials, but the numbers appeared on opposite sides of the screen. The stimuli in the congruent and incongruent conditions were identical for the symbolic and the nonsymbolic comparison tasks. The stimuli for the neutral conditions differed between tasks because in the neutral condition, the irrelevant dimension was controlled to have a distance of zero. Within a single trial, participants were presented with a fixation for 500 milliseconds (ms), then a blank screen for 300 ms. Following this, participants were presented with two arrays (Figure 4.1) for 2000 ms or until a key response was made. Once the participant either made a key response or the 2000 ms was up a blank screen was presented for 500 ms. See the OSF page at https://osf.io/qyczk/.F for a list of the trials.

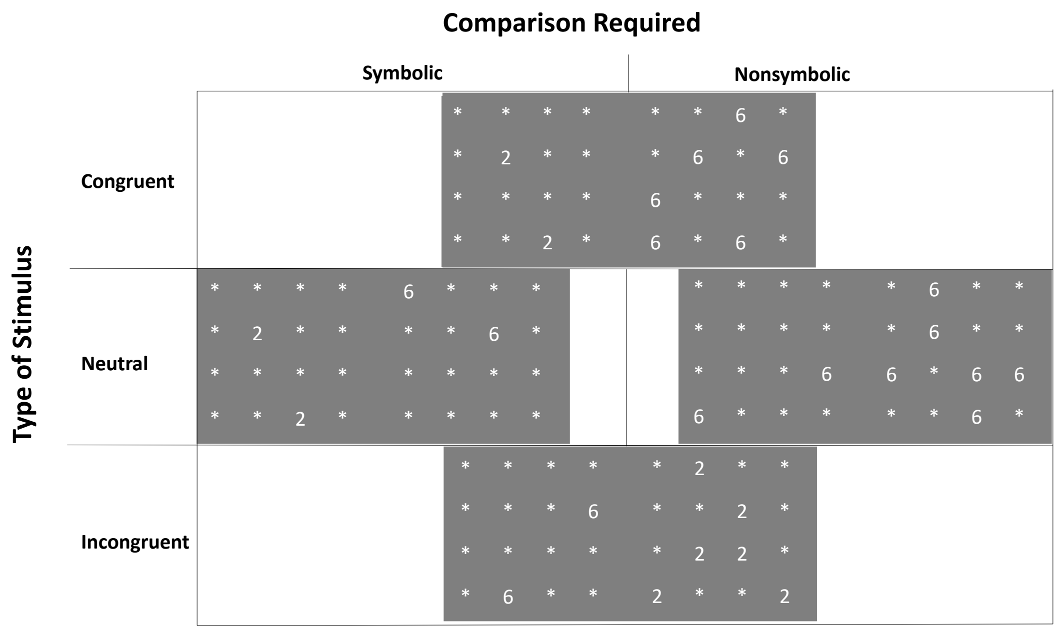

Figure 4.2 Examples of types of stimuli presented. For congruent and incongruent, the same stimuli were used for both the symbolic and the nonsymbolic comparisons. The stimuli for the neutral condition differed for the symbolic and the nonsymbolic comparison conditions.

4.2.2.3 Procedure

All included measures were obtained during a single session that took approximately two hours. During the session, participants completed a series of cognitive tasks including the Symbolic-Nonsymbolic Stroop tasks. The symbolic-nonsymbolic Stroop tasks were always given at the beginning of the session. Only the results from the Symbolic-Nonsymbolic Stroop task are reported here. Participants viewed the stimuli on one of two identical Dell desktop machines that run Windows 8.1. Participants were seated roughly 60-70 cm from the screen, which was an 18.6 by 12.1 inch flat-screen LCD monitor with 1680 x 1050 resolution. All participants first completed both the symbolic and nonsymbolic comparison task, but the order that the participant completed the task was counterbalanced between participants. Each task (symbolic and nonsymbolic) began with a practice block that randomly presented 5 of the 216 stimuli. Feedback was given at the end of the practice block. Participants continued to the actual experiment if they correctly answered 4 out of 5 practice trials (i.e., 80% correct). If the participant did not get at least 80% of the practice block correct the participant redid the practice block. The actual experiment for each task was composed of two blocks. In each block, all 216 stimuli were randomly presented once. The participants got one break between the two blocks.

4.2.3 Experiment 1: Results

Trials with an RT that were + or – 3SD from the mean of the trial type within an individual were considered outliers and removed. This resulted in less than 1% of the RT data being removed. Following this, the RTs for each trial were adjusted to reflect both the speed and accuracy of performance. RTs and error rates were combined to produce an efficiency score using the following formula.

$$Efficency\ Score = \frac{Response\ Time}{1 - Errors}$$

An efficiency score allows for the RTs to remain unchanged on correct trials and increase proportionally with the number of errors. Efficiency scores are often used in the literature (e.g., Sasanguie, Van den Bussche, & Reynvoet, 2012; Simon et al., 2008) as they account for both speed and accuracy. Recently, it has been noted that although efficiency scores do provide a better summary of the findings, these scores increase the variance of the measure, and therefore, it is necessary to further check the data to ensure that the pattern of results for the RT and accuracy is the same (Bruyer & Brysbaert, 2011). In the current study, each of the RT and accuracy produce the same pattern of results as the efficiency score. Consequently, all results will be reported as efficiency scores. The raw data files are publicly available on the Open Science Framework (OSF) at https://osf.io/qyczk/.

A three-way repeated-measures analyses of variance (ANOVA) was conducted to examine the influence of three independent variables (task, congruency, distance) on efficiency scores from the Symbolic-Nonsymbolic Stroop task. Task included two levels (symbolic, nonsymbolic), congruity included three levels (congruent, neutral, incongruent), and distance included six levels (1, 2, 3, 4, 5, 6). All statistical tests were carried out using a two-tailed test with an alpha of .05. Effect sizes were estimated using partial η^2. Mauchly's Test of Sphericity was significant for all main effects and interactions. Therefore, the Greenhouse-Geisser correction was used for all analyses.

4.2.3.1 Effortful Processing

The main effect of task and the interaction between task and distance was used to assess similarities and differences in the effortful processing of symbolic and nonsymbolic numerical magnitudes. These results assess effortful processing because these effects collapse across conditions of congruity, functionally controlling for variability that is attributable to the automatic processing of the irrelevant dimension. Results revealed a significant main effect of task, $F(1, 79) = 49.97$, $p < .001$, $\eta^2 = 0.39$. Specifically, participants were more efficient on the symbolic compared to the nonsymbolic task. There was also a significant two-way interaction between task and distance $F(2, 172) = 373.66$, $p < .001$, $\eta^2 = 0.83$ (Figure 4.3). Post-hoc pairwise comparisons with a Bonferroni correction for multiple comparisons with a critical *p*-value <.05 revealed that distance had a stronger effect on performance on the nonsymbolic task compared to the symbolic task. Specifically, in the nonsymbolic task, all distances were significantly different from each other (p<.001). In the symbolic task, distances 1, 2 and 3 were significantly different from all other distances (p<.001), distance 4 differed from distance 5 at a threshold of p<.05 and from distance 6 at a threshold of p<.01. However, in the symbolic task, distance 5 and distance 6 were not significantly different. Notably, there was a significant main effect of numerical distance $F(2, 190) = 1006.90$, $p < .001$, $\eta^2 = 0.93$, indicating that participants were more efficient at comparing trials with large distances across tasks. However, this main effect should be interpreted with caution due to the significant interaction effects. In sum, these results suggest that the effortful processing of symbols is more efficient and less influenced by numerical distance than the effortful processing on nonsymbolic numerical magnitudes.

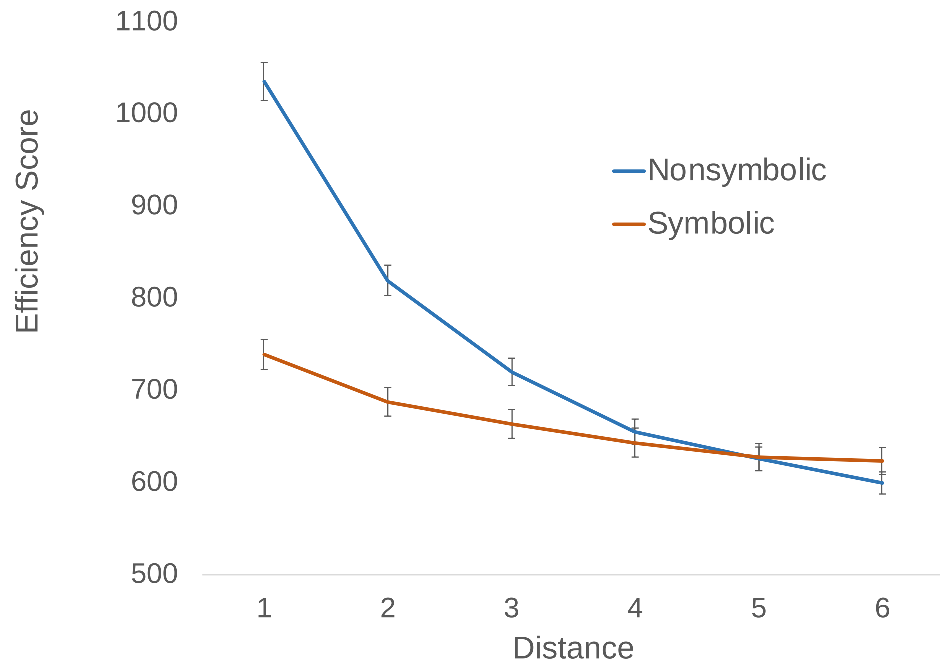

Figure 4.3 This figure depicts the effortful processing of symbols compared to quantities across six numerical distances. Efficiency scores for the symbolic (orange) and nonsymbolic (blue) tasks, collapsing across congruent, neutral and incongruent trials are plotted at all six distances. Error bars represent standard error. This figure highlights the task by distance interaction, which indicates participants are more efficient and less influenced by numerical distance when processing symbolic compared to nonsymbolic numerical magnitudes.

4.2.3.2 Automatic Processing

The main effect of congruity was used to assess whether symbols and quantities influenced each other across tasks. By collapsing across conditions of task and distance, we are controlling for differences in the effortful processing of the relevant dimension and consequently, evaluating only the automatic influence of the irrelevant dimension. Results revealed a significant main effect of congruity $F(1, 106) = 297.64$, $p < .001$, $\eta^2 = 0.79$. Post-hoc pairwise comparisons with a Bonferroni correction for multiple comparisons with a critical p-value $< .05$ showed that congruent, neutral, and incongruent trials all differed significantly from one another. Specifically, participant's performance was strongest on congruent trials and weakest on incongruent trials. This main effect reveals that, regardless of condition (i.e., making symbolic or nonsymbolic comparisons), participants were more efficient at making comparisons when the relevant and irrelevant stimulus dimensions were congruent compared to when they were incongruent with each other. The fact that participants were fastest on the congruent trials suggests that the alignment of magnitude between the relevant and irrelevant dimension improved or facilitated performance. In contrast, the magnitude irrelevant dimension conflicting with the magnitude of the relevant dimension was related to weaker performance. This is evidence of an interference effect. Therefore, it follows to consider whether symbolic and nonsymbolic numerical magnitudes influence each other in the same or distinct ways.

The two-way interaction between task and congruity, and the three-way interaction between task, congruity, and distance were used to examine whether there were differences in the congruity effects between tasks and whether this was modulated by numerical distance. Results revealed that the two-way interaction between task and congruity was not significant, $F(1, 107) = 0.19$, *ns*, $\eta^2 = 0.002$. However, there was a significant three-way interaction between task, congruity, and distance, $F(5, 357) = 34.51$, $p < .001$, $\eta^2 = 0.30$ (Figure 4.4). Descriptive statistics for the three-way interaction are reported in Table 4.1. These results suggest that there is a distance-dependent asymmetry in the automatic influence of symbols and quantities. Post-hoc pairwise comparisons with a Bonferroni correction for multiple comparisons with a critical *p*-value <.05 revealed that at symbols interfered with quantities across all distances, but nonsymbolic interference was distance-dependent. Specifically, nonsymbolic interference was significant for distances 2-6, but not for distance 1 (Figure 4.4, Table 4.2). Related post-hoc pairwise comparisons examining the difference between distances for each condition revealed that in the nonsymbolic task all six distances were significantly different from each other at all congruity levels (p<.001). In contrast, for the symbolic task the distance 5 and 6, did not significantly differ in the congruent condition, distance 4 and 5, as well as 5 and 6, did not significantly differ from each other in the neutral condition, and distance 2, 3, 4, 5, and 6 did not significantly differ from each other in the incongruent condition. All other conditions differed significantly from each other at a threshold of p<.05. This reveals that in addition to the nonsymbolic distance effect being stronger than the symbolic distance effect across congruity conditions, the symbolic distance effects were weakest for the incongruent condition, followed by the neutral condition, and strongest for the congruent. This suggests that the subtle distance effect in the symbolic condition may actually be driven by the automatic influence of quantities.

Table 4.1 Descriptive Statistics for each Condition in Experiment 1.

		Nonsymbolic Task		**Symbolic Task**	
Congruity	**Distance**	*Mean*	*SD*	*Mean*	*SD*
Congruent	1	928.0	195.8	715.8	153.3
	2	761.6	164.9	651.6	132.7
	3	676.7	136.5	618.0	141.9
	4	620.8	128.4	590.8	136.5
	5	597.4	122.1	569.8	124.0
	6	575.9	104.1	561.6	123.5
Neutral	1	1004.2	196.9	739.3	152.0
	2	815.8	161.5	680.1	140.6
	3	707.0	145.2	655.3	143.3
	4	650.6	125.0	627.4	134.8
	5	618.7	106.7	614.1	138.5
	6	594.9	109.3	603.9	126.0
Incongruent	1	1174.3	264.3	762.5	155.1
	2	881.5	156.2	731.8	160.6
	3	777.5	140.0	718.6	151.7
	4	694.8	129.2	712.6	171.2
	5	662.1	127.8	699.4	164.8
	6	628.5	115.9	705.4	177.8

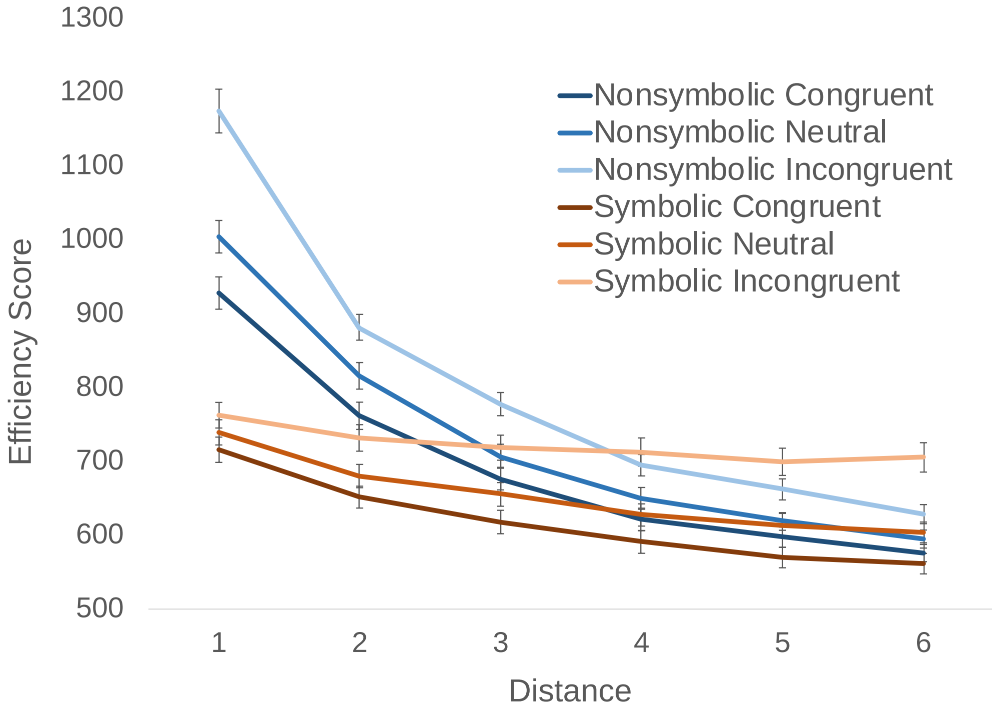

Figure 4.4 This figure depicts efficiency scores for symbolic (orange) and nonsymbolic (blue) tasks at each congruity condition (congruent (darkest), neutral (medium) and incongruent (lightest) across all six distances. Error bars represent standard error of the mean. This figure highlights that at large distances, efficiency scores for congruent, neutral and incongruent conditions differ significantly for both the symbolic and nonsymbolic tasks. However, at small distances, participants have higher efficiency scores (i.e., poorer performance) on the nonsymbolic task than the symbolic task and the difference between congruent, neutral, and incongruent is larger on the nonsymbolic than the symbolic task.

Table 4.2 Bonferroni Corrected Post-hoc Pairwise Comparisons for 3-way Interaction (Task*Congruity*Distance) for Experiment 1.

Task	Distance	Congruity			*Mean Dif*	*SE*	*P-Value*
Nonsymbolic	1	Neutral	vs	Congruent	76.21*	15.28	<.001
		Incongruent	vs	Congruent	246.39*	27.24	<.001
		Incongruent	vs	Neutral	170.18*	26.47	<.001
	2	Neutral	vs	Congruent	54.18*	9.70	<.001
		Incongruent	vs	Congruent	119.90*	13.55	<.001
		Incongruent	vs	Neutral	65.71*	12.64	<.001
	3	Neutral	vs	Congruent	30.27*	5.98	<.001
		Incongruent	vs	Congruent	100.83*	9.91	<.001
		Incongruent	vs	Neutral	70.56*	10.57	<.001
	4	Neutral	vs	Congruent	29.83*	5.87	<.001
		Incongruent	vs	Congruent	73.98*	8.46	<.001
		Incongruent	vs	Neutral	44.15*	6.74	<.001
	5	Neutral	vs	Congruent	21.37*	5.44	<.001
		Incongruent	vs	Congruent	64.70*	7.57	<.001
		Incongruent	vs	Neutral	43.33*	7.26	<.001
	6	Neutral	vs	Congruent	18.99*	3.59	<.001
		Incongruent	vs	Congruent	52.66*	5.08	<.001
		Incongruent	vs	Neutral	33.67*	4.33	<.001
Symbolic	1	Neutral	vs	Congruent	23.50	10.61	0.089
		Incongruent	vs	Congruent	46.70*	9.60	<.001
		Incongruent	vs	Neutral	23.20	10.16	0.075
	2	Neutral	vs	Congruent	28.49*	6.27	<.001
		Incongruent	vs	Congruent	80.21*	7.89	<.001
		Incongruent	vs	Neutral	51.72*	9.81	<.001
	3	Neutral	vs	Congruent	37.33*	4.86	<.001
		Incongruent	vs	Congruent	100.61*	8.50	<.001
		Incongruent	vs	Neutral	63.28*	7.90	<.001
	4	Neutral	vs	Congruent	36.62*	6.30	<.001
		Incongruent	vs	Congruent	121.81*	10.95	<.001
		Incongruent	vs	Neutral	85.19*	9.03	<.001
	5	Neutral	vs	Congruent	44.33*	5.31	<.001

	Incongruent	vs	Congruent	129.60*	13.18	<.001
	Incongruent	vs	Neutral	85.27*	12.25	<.001
	Neutral	vs	Congruent	42.29*	5.61	<.001
6	Incongruent	vs	Congruent	143.79*	14.30	<.001
	Incongruent	vs	Neutral	101.50*	12.43	<.001

Notably, the two-way interaction between congruity and distance from Experiment 1 was also significant, $F(4, 333) = 4.12$, $p < .01$, $\eta^2 = 0.05$. However, these findings are not informative as they collapse across symbolic and nonsymbolic number processing, thereby combining effects of the relevant and irrelevant dimensions for this interaction.

In summary, the results from experiment 1 produce several key findings. First, findings reveal that the effortful processing of symbolic numerical magnitudes is more efficient and less affected by numerical distance compared to the effortful processing of nonsymbolic numerical magnitudes. Second, the results from experiment 1 reveal that symbolic and nonsymbolic numerical magnitudes are both processed automatically. Moreover, the automatic processing of symbolic and nonsymbolic numerical magnitudes influence each other. However, this automatic influence is not symmetrical. Indeed, we find that symbolic numerical magnitudes are processed more automatically than nonsymbolic numerical magnitudes. Specifically, irrelevant symbols influence the processing of quantities more than irrelevant quantities influence the processing of symbols. Additionally, in the nonsymbolic task, numerical distance affects the processing of quantities across all levels of congruity. However, in the symbolic task, the distance effect is greatest for congruent conditions, followed by neutral conditions, and there is barely an effect of distance on incongruent trials. Together, these findings provide evidence to suggest that the systems used to process symbols and quantities are overlapping, as there is evidence that the automatic processing of one format asymmetrically influences the effortful processing of the other format.

The findings from this study included numbers from 1-9. While this is helpful to understand these effects across the full range of single-digit numbers, small and large nonsymbolic numerical magnitudes are thought to be processed using distinct systems

(Hyde, 2011), with small nonsymbolic numerical quantities being processed more similarly to symbols. In view of this, it is necessary to examine whether these results can be replicated when including only large nonsymbolic numerical magnitudes, that the visual system cannot process exactly.

4.3 Experiment 2

4.3.1 Experiment 2: Introduction

Subitizing is a cognitive ability that allows for the fast, automatic, and accurate identification of the quantity of a small set of items (i.e., sets containing 1-4 items) (Mandler & Shebo, 1982; Trick & Pylyshyn, 1994). Large sets (i.e., sets containing 5 or more items) are considered to be in the ‘counting range,’ as these sets are evaluated through the effortful process of counting, or approximate estimation. The quantity of a set of items in the subitizing range is named more quickly and accurately than the quantity of a set of items in the counting range (Kaufman, Lord, Reese, & Volkmann, 1949; Trick & Pylyshyn, 1993). Prior research has refuted the idea that there is a single estimation system used to process quantities in both the subitizing and counting range and instead supported the notion that humans possess a dedicated mechanism for processing small subitizable quantities (Revkin, Piazza, Izard, Cohen, & Dehaene, 2008). Research has revealed that the processing of small quantities (i.e., 1-4) is supported by a parallel individuation system, used to track objects in order to identify the exact number of items in small sets. In contrast, research suggests that an analogue magnitude system (often referred to as an approximate number system (ANS)) supports the processing of quantities with five or more objects. The analogue magnitude system uses approximate estimation to process larger quantities (For review see: Hyde, 2011). We predict that quantities in the subitizing range, that are processed using the PI system are processed in a way that is more similar to symbols. Consequently, we predict that the differences between the effortful automatic processing of symbols and quantities will be more extreme for quantities in counting range, processed using analogue magnitude system.

In view of the fact that humans automatically perceive the exact quantity of a set in the subitizing range, it is conceivable that nonsymbolic quantities in the subitizing range are more likely to activate exact representations of symbolic numerical magnitudes compared to nonsymbolic numerical magnitudes in the counting range. The stimuli in experiment 1 included all single-digit numerical magnitudes (i.e., quantities one to nine). Consequently, results from experiment 1, suggesting that symbolic and nonsymbolic numerical magnitudes influence each other during the Stroop task, could be driven by quantities in the subitizing range. In order to confirm that the Stroop effect (i.e., the finding that symbolic and nonsymbolic numerical magnitudes influence each other) is not simply due to the fact that quantities in the subitizing range are activating exact symbolic representations it is critical to replicate this paradigm using only numbers in the counting range. Therefore, in experiment 2, an independent sample of participants completed a modified version of the Symbolic-Nonsymbolic Stroop task that included only numbers in the counting range (i.e., 5-9).

4.3.2 Experiment 2: Method

4.3.2.1 Participants

Sixty-three healthy adult participants were recruited at the University of Western Ontario in London, Ontario. Four participants were excluded from analyses due to poor accuracy (< 70% on at least one trial type). Therefore, all analyses for experiment two include 59 participants (M_{age}=23.86, SD_{age}=3.79; 20 males, 39 females). Participants provided written consent before participating in the study. The session took approximately one hour and participants were compensated $5 CAD per half-hour (average $10 CAD total). All procedures were approved by the University of Western Ontario Non-medical Research Ethics Board (See Appendix A).

4.3.2.2 Materials

4.3.2.2.1 Symbolic-Nonsymbolic Stroop Task

Each participant completed both the symbolic and nonsymbolic version of the Symbolic-Nonsymbolic Stroop task with all the same parameters described in experiment one. The trial list for experiment two differed from experiment one. Namely, the task only included both symbols and quantities in the counting range (5-9). As with experiment 1, the stimuli, code to create the stimuli, and the OpenSesame experiments, which include the trial lists, are available at on the Open Science Framework (OSF) at https://osf.io/qyczk/.

Participants were randomly presented with two blocks of 36 trials repeated twice each (144 total trials) on the symbolic task and on the nonsymbolic task. Of the 36 trials, 12 stimulus pairs were congruent, 12 were incongruent, and the remaining 12 trials were neutral. Each of the 12 trials consisted of 4 trials at each of distance 1-3. Notably, half of the 36 trials, had the same numbers as the other half, but the numbers appeared on opposite sides of the screen. The stimuli in the congruent and incongruent conditions were identical for the symbolic and the nonsymbolic tasks. The stimuli for the neutral conditions differed between tasks because in the neural condition, the irrelevant dimension was controlled to have a distance of zero. There were two versions of the task that used different magnitudes for the trials. The versions were counterbalanced between participants. Notably, both version A and version B of the paradigm are available on the Open Science Framework (OSF) at https://osf.io/qyczk/.

4.3.2.3 Procedure

All included measures were obtained during a single session that took approximately one hour, where participants completed a series of basic number processing tasks including the Symbolic-Nonsymbolic Stroop tasks with numbers only on the counting range. Only the results from the counting Symbolic-Nonsymbolic Stroop task are reported here. The procedure is the same as for experiment one with the exception that participants were randomly presented with two blocks containing the same 36 trials for each task. The participants got one break between the two blocks.

4.3.3 Experiment 2: Results

As reported in experiment 1, the RT and accuracy produce the same pattern of results as the efficiency score for experiment 2. Consequently, all results will be reported as efficiency scores. As with experiment 1, the raw data files for experiment 2 are publicly available on the Open Science Framework (OSF) at https://osf.io/qyczk/.

A three-way repeated-measures analyses of variance (ANOVA) was conducted to examine the influence of three independent variables (task, congruency, distance) on efficiency scores from the Symbolic-Nonsymbolic Stroop task. Task included two levels (symbolic, nonsymbolic), and congruity included two levels (congruent, neutral, incongruent), and distance included three levels (1, 2, 3). Descriptive statistics for each condition are reported in Table 4.3. All statistical tests were carried out using a two-tailed test with an alpha of .05. Effect sizes were estimated using partial η^2. Mauchly's Test of Sphericity was significant for the main effect of distance, and the following interactions: task*distance, congruity*distance, task*congruity*distance. The Greenhouse-Geisser correction was used for all analyses that violated the assumption of sphericity. As with experiment 1, the main effect of task and interaction between task and distance was used as a measure of effortful processing, as these analyses collapse across congruity conditions, therefore controlling for the effect of the irrelevant dimension. The main effect of congruity was used to assess the automatic effect of processing, as this effect collapses across variability associated with effortful processing and distance. Finally, the two-way interaction between congruity and task, and the three-way interaction between congruity, task and distance were used to assess whether there are asymmetries in the automatic processing of symbolic and nonsymbolic numerical magnitudes.

Table 4.3 Descriptive Statistics for each Condition in Experiment 2

		Nonsymbolic Task		**Symbolic Task**	
Congruity	**Distance**	*Mean*	*SD*	*Mean*	*SD*
Congruent	1	1324.8	336.5	666.0	144.9
	2	1000.8	243.6	619.1	136.0
	3	880.8	170.9	606.8	113.7
Neutral	1	1421.7	441.5	689.4	149.1
	2	1054.4	212.7	642.2	133.8
	3	932.2	181.3	620.3	126.0
Incongruent	1	1604.1	406.6	699.7	152.0
	2	1159.7	258.7	663.8	186.5
	3	1031.1	176.0	649.8	135.1

4.3.3.1 Effortful Processing

The main effect of task and the interaction between task and distance was used to assess similarities and differences in the effortful processing of symbols and quantities. The significant main effect of task indicated that participants were more efficient on the symbolic compared to the nonsymbolic task $F(1, 58) = 553.52$, $p <.001$, $\eta^2 = 0.91$. There was also significant two-way interaction between task and distance, $F(1, 84) = 213.72$, $p <.001$, $\eta^2 = 0.79$ (Figure 4.5). Post-hoc pairwise comparisons with a Bonferroni correction for multiple comparisons with a critical *p*-value <.05 revealed that distance had a stronger effect on performance on the nonsymbolic task compared to the symbolic task, as discovered in experiment 1. Specifically, the distances in the nonsymbolic task were all significantly different from each other with at a p<.001. In the symbolic task, distance 1 was significantly different from distance 2 and distance 3 (p<.001), but there was no significant difference between distance 2 and distance 3. Notably, the main effect of numerical distance was also significant $F(2, 94) = 297.73$, $p <.001$, $\eta^2 = 0.84$, with participants most efficient at distance 3 and least efficient at distance 1 across tasks, but this main effect should be interpreted with caution in view of the significant interactions. Together, these results converge with results from experiment 1 to suggest that symbolic numerical magnitudes are processed more efficiently and are less affected by numerical distance, compared to nonsymbolic numerical magnitudes.

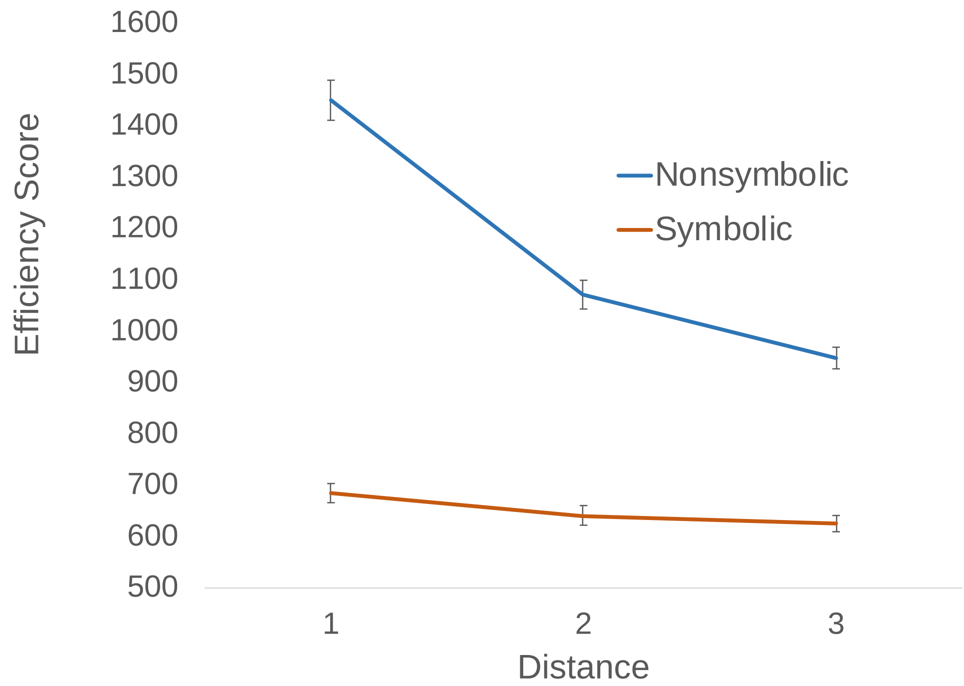

Figure 4.5 This figure depicts the effortful processing of symbols compared to quantities in the counting range across three numerical distances. Efficiency scores for symbolic (orange) and nonsymbolic (blue) task, collapsing across congruent, neutral and incongruent trials are plotted across all three distances. Error bars represent standard error. This figure highlights the task by distance interaction, which indicates that participants are more efficient and less influenced by numerical distance when processing symbolic compared to nonsymbolic numerical magnitudes.

4.3.3.2 Automatic Processing

The main effect of congruity was analyzed to examine whether symbols and quantities influenced each other across tasks. The significant main effect of congruity revealed that congruent, neutral, and incongruent trials differed significantly from one another, $F(2, 116) = 59.18$, $p < .001$, $\eta^2 = 0.51$. Post-hoc pairwise comparisons with a Bonferroni correction for multiple comparisons and a critical p-value <.05 showed that congruent, neutral, and incongruent trials all differed significantly from one another. Specifically, participant's performance was strongest on congruent trials and weakest on incongruent trials. This main effect indicates that at some level of processing symbolic and nonsymbolic numerical magnitudes influence each other, even when only including numbers in the counting range. Therefore, we examine whether this influence of symbolic and nonsymbolic numerical magnitudes on each other is symmetrical for numbers in the counting range.

The two-way interaction between task and congruity, and the three-way interaction between task, congruity, and distance were used to examine whether there were differences in the congruity effects between tasks and whether these differences were modulated by numerical distance. In experiment 2, the two-way interaction between task and congruity was significant, $F(2, 116) = 26.09$, $p = <.001$, $\eta^2 = 0.31$. Post-hoc pairwise comparisons with a Bonferroni correction for multiple comparisons with a critical *p*-value $<.05$ revealed that symbols influence the processing of quantities more than quantities influence processing of symbols, across all distances (Figure 4.6, Table 4.4). Unlike the results from experiment 1, the three-way interaction between task, congruity, and distance, was not significant in experiment 2 $F(2, 136) = 2.36$, *ns*, $\eta^2 = 0.04$.

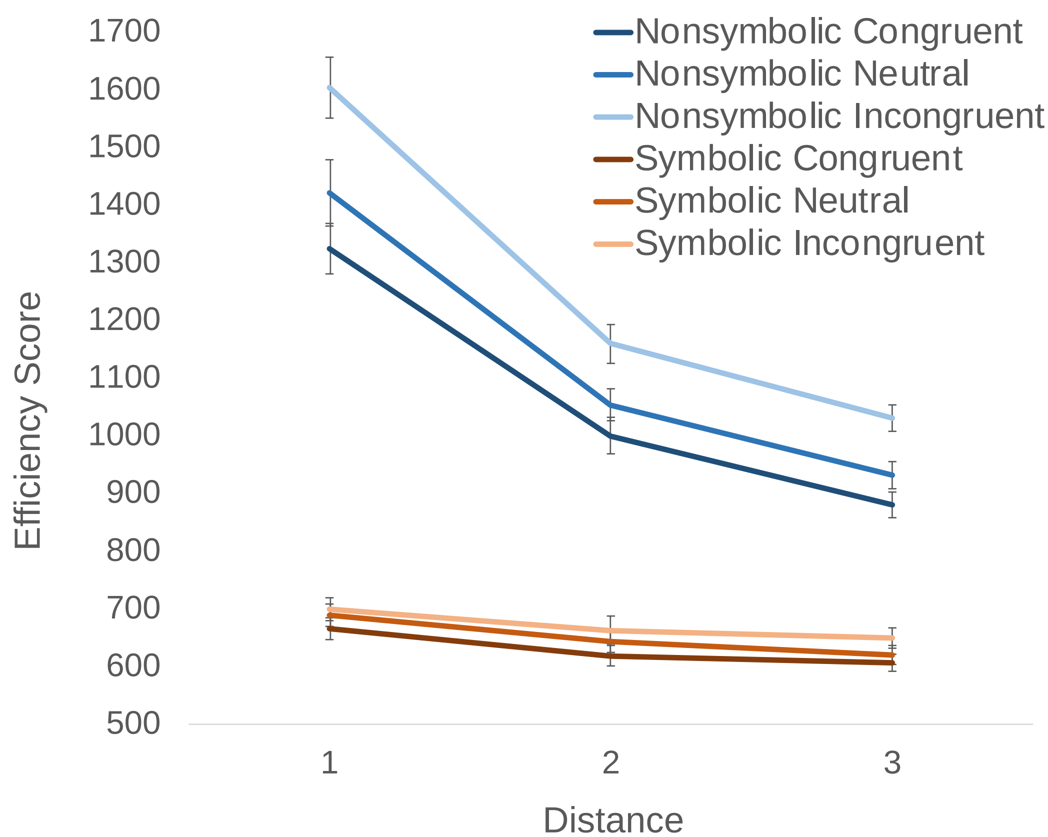

Figure 4.6 This figure depicts efficiency scores for symbolic (orange) and nonsymbolic (blue) Stroop tasks when the symbolic and nonsymbolic stimuli are congruent (darkest), neutral (medium) and incongruent (lightest) across all three distances. Error bars represent standard error. This figure highlights that participants have higher efficiency scores (i.e., poorer performance) on the nonsymbolic task than the symbolic task and the difference between congruent, neutral, and incongruent is larger on the nonsymbolic than the symbolic task, across all numerical distances.

Table 4.4 Bonferroni Corrected Post-hoc Pairwise Comparisons with a 2-way Interaction between Task and Congruity for Experiment 2

Task	**Congruity**			*Mean Dif*	*SE*	*P-Value*
Nonsymbolic	Neutral	vs	Congruent	67.267*	19.35	<.01
	Incongruent	vs	Congruent	196.158*	23.35	<.001
	Incongruent	vs	Neutral	128.891*	21.40	<.001
Symbolic	Neutral	vs	Congruent	20.012*	4.06	<.001
	Incongruent	vs	Congruent	40.455*	5.95	<.001
	Incongruent	vs	Neutral	20.442*	5.38	<.01

The two-way interaction between congruity and distance was not significant in experiment 2, $F(2, 135) = 1.33$, *ns*, $\eta^2 = 0.02$. Critically, as with experiment 1, these findings are not informative as they collapse across symbolic and nonsymbolic number processing and congruity, thereby combining effects of the relevant and irrelevant dimensions.

4.4 Discussion

A fundamental question in the field of numerical cognition is: are symbolic numbers processed in the same way as nonsymbolic numerical magnitudes? To address this question, we developed and used a Symbolic-Nonsymbolic Stroop paradigm to assess effortful and automatic processing of symbolic and nonsymbolic numbers. By examining whether nonsymbolic and symbolic representations automatically influence one another we can probe how strongly they are linked. If they are strongly linked, then processing one should activate the other. If, however, they are disconnected then they should not influence each other, or the influence should be asymmetrical. In the Symbolic-Nonsymbolic Stroop paradigm we used to probe these possibilities, participants were asked to compare adjacent arrays of symbols (e.g., 4444 vs 333) and instructed to indicate the side containing *either* the greater quantity of symbols (nonsymbolic task) or the side containing the symbol with the greater numerical magnitude (symbolic task). This paradigm evaluates both processing of the relevant dimension (i.e., the dimension the participant is instructed to attend to) as well as the degree to which the irrelevant stimulus condition influences judgments being made on the relevant condition. For example, when comparing which side contains the numerically larger symbol (i.e., the relevant dimension), does the actual number of symbols present (i.e., the irrelevant dimension) influence performance? Using this approach, we found that symbolic numerical magnitudes were processed more automatically than nonsymbolic numerical magnitudes as both the relevant and the irrelevant dimensions.

Indeed, across conditions, participants performed better (i.e., responded faster and more accurately) on the symbolic task compared to the nonsymbolic task. This suggests that as the relevant dimension, symbols are processed more automatically. Additional asymmetries were observed through much stronger distance effects during nonsymbolic judgments compared to symbolic judgments, especially when comparisons were made in the counting range. Critically, unlike other paradigms, this task has the capacity to examine automaticity of processing symbolic and nonsymbolic numerical magnitudes when these number formats act as the irrelevant dimensions. By including a neutral condition in our task, we were able to measure the extent to which the irrelevant dimension either helped (facilitated) or hindered (interfered) task performance on the relevant dimension. Our findings revealed an asymmetry in the interference and facilitation patterns of symbolic compared to nonsymbolic numerical judgments. Symbols, as compared to nonsymbolic numerical magnitudes, led to both greater facilitation and interference effects. Notably, when including trials in both the subitizing and counting range, as was the case in experiment 1, this asymmetry in the congruity effects between the symbolic and nonsymbolic task is stronger for trials with small distances. Taken together, our findings demonstrate that symbolic numerical magnitudes are processed more automatically than nonsymbolic numerical magnitudes as both the relevant and irrelevant dimensions. In what follows, we discuss how this finding indicates asymmetric processing of symbolic and nonsymbolic numerical magnitudes and suggest differences in the ways in which each format is processed and potentially represented.

4.4.1 Congruity Effects

Regardless of condition (i.e., making symbolic or nonsymbolic comparisons), participants were more efficient at making comparisons when the two stimulus dimensions were congruent compared to when they were incongruent with each other. Furthermore, in the neutral condition, participants' performance was in between that obtained from the other two conditions, suggesting that congruent conditions facilitate performance and incongruent conditions interfere with performance. These findings are noteworthy in that they show the powerful effect of the irrelevant stimulus on one's ability to make basic numerical judgments. One interpretation of these findings is that symbolic and nonsymbolic numerical magnitudes are processed in parallel and potentially under the same regulatory system (e.g., see Henik & Tzelgov, 1982). Applying this line of reasoning to the current study, if symbolic and nonsymbolic numerical magnitudes bore no relation to one another and were processed by independent systems entirely, one would not expect to find evidence of facilitation or interference effects. In other words, if symbolic and nonsymbolic numbers were processed using two entirely distinct systems there would not be a Stroop-effect. Therefore, our findings provide some evidence of parallel or simultaneous processing of symbolic and nonsymbolic magnitudes. However, these findings should be interpreted with caution in light of the many significant interactions discussed below. Nonetheless, these findings align with a large body of theory and empirical findings demonstrating a close relation between number symbols and the nonsymbolic numerical magnitudes they represent (e.g., Cantlon et al., 2009; Dehaene, 2007; Dehaene et al., 1998; Nieder & Dehaene, 2009; Piazza et al., 2007).

However, our findings also challenge this line of research and instead suggest that perhaps there are key differences in the ways symbolic and nonsymbolic numerical magnitudes are processed. Indeed, our results revealed that in comparison to nonsymbolic numerical magnitudes, number symbols (i) were processed more efficiently (i.e., faster and more accurately) as the relevant dimension, (ii) had a greater influence on task performance as the irrelevant dimension, and (ii) were less influenced by numerical distance between magnitudes as the relevant and irrelevant dimension. Notably, distance only moderated the relationship between task and congruity when including all numbers from 1-9, but not when only examining numbers in the counting range. We now address each one of these points in turn and discuss the findings in terms of evidence of asymmetrical processing of symbolic and nonsymbolic numerical magnitudes.

4.4.2 Effortful processing: Effects of the Relevant Dimension

Overall, participants performed better (i.e., were more efficient) comparing symbolic compared to nonsymbolic numerical magnitudes. Although other researchers have reported similar findings (e.g., see Buckley & Gillman, 1974; Lyons & Beilock, 2009), this is the first study to do so within the context of a Symbolic-Nonsymbolic Stroop paradigm, where the task-irrelevant influence of one dimension on the other (e.g., symbolic on nonsymbolic) can be measured. In fact, our results run counter to findings from the standard Numerical Stroop paradigm produces a size-congruity effect. Recall that the standard paradigm has participants compare Hindu-Arabic digits based on either the physical size of the numerals (e.g., 3 vs. 5) or the numerical value. Results from this paradigm show that participants are faster at judging physical size and are less influenced by the symbolic value of the digits than the size. The most straightforward explanation for the discrepancy in findings is that in our task the nonsymbolic condition involves serial processing of discrete units (i.e., the total number of number symbols present). Conversely, the symbolic task can be approached by attending to a single unit (i.e., any given symbol present). Thus, both the physical size and symbolic task within the traditional Numerical Stroop paradigm is more akin to our symbolic task in which comparisons can be made by attending to a single stimulus. This discrepancy between the current study and previous Numerical Stroop paradigms that produce a size congruity effect provides evidence in support of the notion that the quantity discrimination task in the Symbolic-Nonsymbolic Stroop paradigm is capturing more than processing of continuous magnitudes (e.g., area), an inherent confound of nonsymbolic number comparison tasks (For review see, Leibovich & Henik, 2013). If participants were solving the nonsymbolic task in the current study using purely a physical size strategy, one would predict that the results would closely mirror the Size Congruity Effect, namely that like participants are better at processing size than symbols, participants would be more efficient at processing nonsymbolic numerical magnitudes compared to symbols. Instead, we find the reverse pattern of results, namely that as the relevant dimension, symbols are processed more efficiently than nonsymbolic numerical magnitudes. Although the finding that humans are better at effortfully processing symbols compared to quantities is neither new (e.g, Buckley & Gillman, 1974; Lyons & Ansari, 2009), nor surprising, it highlights the general efficiency and cultural utility of symbols and number symbols more specifically (see Núñez, 2017).

4.4.3 Automatic Processing: Effects of the Irrelevant Dimension

As previously discussed, results revealed a congruity effect (i.e., greater efficiency in processing congruent compared to incongruent trials) in both the symbolic and nonsymbolic comparison conditions. Indeed, participant's performance on comparisons in both the symbolic task and the nonsymbolic task was most efficient when the two stimulus dimensions were congruent, followed by when they were neutral, and participants performance was worst on incongruent conditions. Therefore, both symbols and the nonsymbolic numerical magnitudes that they represent are processed as the irrelevant dimension and influence number processing of the relevant dimension. A discussed above, the finding that the irrelevant stimulus influences the relevant stimulus provides support for the idea that there is some parallel processing of symbols and quantities, as there would be no effect of the irrelevant stimulus on the relevant stimulus (i.e., no Symbolic-Nonsymbolic Stroop effect) if symbolic and nonsymbolic numerical magnitudes were processed in serial or using two entirely distinct systems. Therefore, the presence of a Stroop effect in the current study supports the idea that symbolic and nonsymbolic numerical magnitudes are processed simultaneously at some stage of processing.

Critically, however, our results also revealed important differences in how symbols influenced and interfered with judgments of nonsymbolic numerical magnitudes compared to the way that nonsymbolic numerical magnitudes influenced and interfered with symbolic judgments. That is, irrelevant number symbols were found to have a much larger impact on performance compared to when nonsymbolic numerical magnitudes acted as the irrelevant dimension. Although many studies have reported that symbols influence the processing of quantities (Bush et al., 1998; Francolini & Egeth, 1980; Morton, 1969; Pavese & Umiltà, 1998, 1999; Windes, 1968), relatively few have examined whether quantities interfere with symbolic processing (Flowers, Warner, & Polanski, 1979; Furman & Rubinsten, 2012; Naparstek & Henik, 2010, 2012; Naparstek et al., 2015; Pansky & Algom, 2002). The only other study to quantify both symbolic and nonsymbolic interference required participants to compare a quantity to a symbolic referent (Naparstek & Henik, 2010). This study revealed that symbols interfered with quantity processing regardless of task demands, whereas the interference of quantity depended on the task. Results from the current study extend finding this to reveal that this asymmetry in the automatic processing of symbols and quantities is present even in a task that does not require participants to compare the nonsymbolic numerical magnitude to a symbolic referent. Therefore, findings from the current study align with previous research to suggest that while there is some overlap in the way that symbolic and nonsymbolic numerical magnitudes are processed, symbols seem to more consistently influence the processing of nonsymbolic numerical magnitudes.

4.4.4 Influence of Numerical Distance

As discussed above, participants perform better on comparative judgments of symbolic compared to nonsymbolic numerical magnitudes across all distances. However, results from the current study also highlight that in addition to symbols being processed more efficiently than nonsymbolic numerical magnitudes, the effortful processing of symbols is less influenced by numerical distance. This finding from the current study, namely, that nonsymbolic processing is more influenced by distance than symbolic number processing is has been previously reported in the literature in both adults and children (e.g., Buckley & Gillman, 1974; Butterworth, 2005; Furman & Rubinsten, 2012; Holloway & Ansari, 2010; Holloway & Ansari, 2008, 2009; Holloway et al., 2010; Moyer & Landauer, 1967; Rubinsten, Henik, Berger, & Shahar-Shalev, 2002).

Several models for this discrepancy of the effect of numerical distance on effortful symbolic and nonsymbolic number processing have been proposed. A seminal computational model was put forward that suggests that symbolic and nonsymbolic numerical magnitudes are transformed into cardinal representation (i.e., place-coded) by different pathways (Verguts & Fias, 2004). Specifically, nonsymbolic numbers are transformed into cardinal representations through a noisy process referred to as 'summation coding.' The noise in this process proportionally relates to the number of inputs being "summed." In contrast, the summation step of this model is not required for processing symbolic numbers, leading to sharper representations for symbolic numbers (Verguts & Fias, 2004). This computational model, which has been supported with empirical neuroimaging data (Holloway et al., 2010; Lyons et al., 2014; Piazza et al., 2007; Roggeman et al., 2007), provides a compelling explanation for the discrepancies found in the current data between the way that distance modulates the effortful processing of symbolic compared to nonsymbolic numerical magnitudes. Notably, there are other explanations for the differences between the processing of symbolic and nonsymbolic numerical magnitudes. Converging recent behavioural data has indicated that the similar behavioural effects observed in different formats of numerical magnitudes (i.e., symbolic and nonsymbolic) do not correlate with each other (Holloway & Ansari, 2009; Krajcsi et al., 2016; Lyons, Nuerk, & Ansari, 2015), and may, in fact, be supported by two similar, but distinct representational systems. Indeed, while nonsymbolic numerical magnitudes are likely processed using an evolutionarily ancient analogue magnitude system, where the ratio of the stimuli's intensity affects performance (Weber's law) (Moyer & Landauer, 1967) the processing of symbols is likely supported by a different more exact system. A proposed system that may support symbolic numerical magnitudes is the discrete semantic system (DSS) (Krajcsi et al., 2016). In a DSS, symbolic numerical magnitudes are stored within a large semantic network, with each symbolic numerical magnitude acting as a node within that network. A DSS would produce a 'distance effect' because the strength of the associations between symbolic numerical magnitudes (i.e., nodes) would correlate with the strength of the semantic relations between the numbers (Krajcsi, 2017; Krajcsi et al., 2016). Evidence that symbolic numerical magnitudes may be supported by a DSS rather than an approximate magnitude system has accumulated both behaviourally (Krajcsi et al., 2016, 2018) and at the neural level of analysis (Lyons & Beilock, 2018). Data from the current study cannot discern between various theories predicting what representations might underpin symbolic compared to nonsymbolic numerical magnitudes. However, these data do provide support for the growing body of evidence indicating that there are striking differences in the way that symbols and nonsymbolic numerical magnitudes are effortfully processed.

The results from the current study provide some evidence to suggest that there may be an asymmetry between symbolic and nonsymbolic numerical magnitudes in the way that distance modulates the influence of the irrelevant dimension. In experiment 1, distance affects the influence of irrelevant quantities during the symbolic comparison more than distance modulates the influence of irrelevant symbols during the nonsymbolic comparison task. More specifically, numerical distance most strongly affects the processing of symbolic numerical magnitudes when the magnitude of the symbol and the quantity are congruent, suggesting that the influence of the congruent quantity may, in fact, be responsible for the distance effect. Interestingly, previous research that has examined whether distance influences the performance on nonsymbolic naming tasks and tasks that require participant to refer to a symbolic referent revealed that when the symbols were numerically close to the quantity that the participants had to verbally name, there was a larger interference effect (Furman & Rubinsten, 2012; Naparstek & Henik, 2010, 2012; Pavese & Umiltà, 1998, 1999). Critically, in experiment 2, where only numbers in the counting range were included, distance does not significantly modulate the automatic processing of symbols or nonsymbolic numerical magnitudes. Instead, symbols influenced the processing of quantities more than quantities influenced the processing of symbols across all distances. In view of this, the current data suggest that numerical distance does not influence the automatic processing of magnitude, for numbers in the counting range. This null effect of distance on the automatic processing of magnitude in the counting range may be due to the fact that by reducing the range of numbers included, we removed conditions where the effect of distance on the automatic processing of symbols and quantities diverged. Indeed, the three-way interaction from experiment 1 was driven by the difference between automatic processing of symbols and quantities at distance 4, 5 and 6. This suggests that distance may differentially relate to automatic processing of symbols compared to quantities, but only in conditions where the two numbers being compared have a large numerical distance and include magnitudes both in the subitizing and counting range. This finding, that distance did not modulate the degree to which quantities influence the processing of symbols, in the counting range, provides further evidence that nonsymbolic numerical magnitudes do not influence the processing of numerical symbols. Indeed, even quantities with the strongest salience (i.e., quantities with large distances), in the counting range, do not influence effortful symbolic number processing. Together, this research provides compelling evidence that symbols and quantities are processed using similar, but ultimately distinct processing systems.

4.4.5 Interpretations and Future Directions

Taken together, our results provide strong evidence for asymmetrical processing of symbolic and nonsymbolic numerical magnitudes. Specifically, when we process nonsymbolic numerical magnitudes, symbolic representations have an influence. However, when we process symbolic magnitudes, nonsymbolic representations of numerical magnitudes have a negligible effect. A predominant view in the field of numerical cognition has been that symbolic number representations are formed by simply attaching symbols to analogue nonsymbolic quantity representations (e.g., Cantlon, 2012; Dehaene, 2007, 2008; Feigenson, 2007; Lyons & Ansari, 2009; Nieder & Dehaene, 2009; Piazza, Pinel, Le Bihan, & Dehaene, 2007). In recent years, it has been suggested that number symbols constitute a separate system in which processing symbols can be done independently from accessing nonsymbolic representations of the quantities the symbols represent. Instead, symbols may be understood based on their associations with other symbols (For a comprehensive review see, Núñez, 2017). This view has been supported by recent behavioural and neuroimaging research, including chapters 2 and 3 of the current thesis, that reports that processing of symbolic numbers is at least somewhat distinct from processing quantities (Bulthé et al., 2014; Cohen Kadosh, 2008; Lyons et al., 2012, 2014; Lyons & Beilock, 2018). The finding from the current study, that symbols are processed more automatically than the quantities that they represent provides evidence that supports the notion that symbols may not simply be labels for pre-existing representations of quantities. Indeed, the findings from the current study suggest that the human mind does not need to access a representation of a nonsymbolic numerical magnitude to *automatically* process the semantic meaning of a number symbol. Instead, data from the current study provides evidence in support of the theory that symbols may themselves be supported by culturally acquired automatic semantic representations (Lyons & Beilock, 2018; Núñez, 2017). This convergent body of evidence that suggests that adults process symbols more automatically than nonsymbolic numerical magnitudes, introduces an important developmental question. Namely, it is of great importance to learn how symbols are learned, and when in development symbols become automatic. A longstanding question in the field of numerical cognition has been, 'how do symbols acquire meaning?' However, based on this data, an equally important follow-up question is 'when does the symbolic system become independent?' The use of the Symbolic-Nonsymbolic Stroop task in a developmental sample is ideally suited to answer this question, as it can be used to illuminate how the representational precision (i.e., distance effects) of symbols and quantities at different levels of processing (i.e., effortful and automatic) change, and likely diverge, across developmental time.

4.4.6 Conclusions

In order to further our understanding of the association between evolutionary ancient, nonsymbolic representations of numerical magnitudes and culturally constructed symbolic representations, the current study examined whether the effortful and the automatic processing of symbolic and nonsymbolic numerical magnitudes are the same or distinct using a Symbolic-Nonsymbolic Stroop paradigm. Results revealed that regardless of the task, participants were more efficient at making comparisons when the two stimulus dimensions were congruent compared to incongruent. This is could be taken to suggest that at some stage of processing symbolic and nonsymbolic numbers are processed in parallel; however, due to the fact that the interaction terms are significant, this finding should be interpreted with caution. Interaction effects from the current study revealed asymmetries in both the automatic and effortful processing of symbolic and nonsymbolic numerical magnitudes. The key finding from the current study is that symbols influenced nonsymbolic numerical magnitude processing more than nonsymbolic numerical magnitudes influenced the processing of numerical symbols. This highlights that there is an asymmetry in the way that the human mind processes symbols and quantities. Further support for this idea that symbols and quantities are processed distinctly is that the effortful processing of symbols was more efficient and less affected by numerical distance than quantities. Additionally, numerical distance modulated nonsymbolic interference more than it modulated symbolic interference when including all numbers (1-9). However, numerical distance did not influence the automatic interference of symbols or quantities for numbers in the counting range. These data provide support for the idea that there is an asymmetry in the way that humans process symbolic compared to nonsymbolic numerical magnitudes, even during non-effortful, automatic processing. Together, these findings, that symbols are processed more automatically than numerically equivalent nonsymbolic numerical magnitudes, suggests that processing symbols do not require accessing a representation of quantity. Instead, it seems that the human mind has the capacity to *automatically* process the semantic meaning of a number symbol. These findings contribute to efforts to forge a deeper understanding of how the mind forms a symbolic number processing system that is independent of the approximate, analogue magnitudes that the symbols represent.

4.5 References

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Chapter 5

5 Children's Verbal Number Knowledge Influences Their Attention to Numerical Quantity

5.1 Introduction

5.1.1 Learning Verbal Number Words

The ability to count a set of objects is a foundational skill that supports many mathematical concepts and procedures. The process of learning to count involves learning the number words sequence (Fuson, Richards, & Briars, 1982) and acquiring several key principles of counting (Gelman & Gallistel, 1978). It typically takes children several years to master counting skills. At roughly two years of age, children have learned the count sequence by rote, but do not yet understand the meaning of these verbal number words (Wynn, 1990; Wynn, 1992). It typically takes children two to three years from the time they master the count list to acquire the cardinal principle, namely the understanding that the last number counted when counting a set, refers to the total number of objects within that set (Gelman & Gallistel, 1978). Children who do not know the cardinal meaning of any number words are referred to as "pre-knowers." Following this, children learn the exact number word meanings of small numbers (i.e., numbers 1-4) in predictable stages before they acquire the cardinal principle (Wynn, 1992). Children who know the meaning of the word one are referred to as "one-knowers." Several months later, children progress to being "two-knowers". Over time, children become "three-knowers" and some studies report the presence of "four-knowers." Children who know the meaning of the verbal number words one to four, but not the cardinal principle, are collectively referred to as "subset-knowers". Cardinal Principle knowers (CP-knowers) are qualitatively different from subset knowers in that they can generate cardinality for all numbers using their knowledge of the cardinal principle (Le Corre & Carey, 2007). It is only once children have acquired the cardinal principle that they are considered to understand the meaning of number words. The acquisition of the cardinal principle is a major milestone in forming numerical understanding and predicts later mathematical abilities (Geary et al., 2018).

5.1.2 Linking Number Words to Quantities

It has been heavily debated whether acquiring the cardinal principle is a cause or a consequence of the ability to process nonsymbolic quantities (e.g., Batchelor, Keeble, & Gilmore, 2015; Dehaene, 2007; Gunderson et al., 2015; Le Corre & Carey, 2007; Mix, 1999, 2008; Mussolin, Nys, Leybaert, & Content, 2014; Negen & Sarnecka, 2015; Shusterman et al., 2016, 2017; Slusser & Sarnecka, 2011; Slusser, Ditta, & Sarnecka, 2013; Wagner & Johnson, 2011). Previous studies have shown that children who have acquired the cardinal principle are more successful than pre-knowers and subset-knowers in several nonsymbolic number tasks (Abreu-Mendoza, Soto-Alba, & Arias-Trejo, 2013; Mussolin, Nys, Content, Leybaert, & Leybaert, 2014; Shusterman et al., 2016; Wagner & Johnson, 2011). For example, pre-school aged children's knowledge of the cardinal principle related to their ability to discriminate between arrays of quantities (Wagner & Johnson, 2011). Similarly, when asked to sort cards based on colour, shape and quantities, all children could sort based on colour and shape, but only CP-knowers were able to sort based on quantity (Slusser & Sarnecka, 2011). Critically, other research has hinted at the idea that some children are able to link verbal number words onto small sets, even before they have acquired the cardinal principle (Le Corre & Carey, 2007). Specifically, some children are able to map between nonsymbolic quantities and the number words that they stood for, even if they do not yet grasp the cardinal principle more generally (Batchelor, Keeble, et al., 2015; Mix, 1999, 2008). Notably, due to small sample sizes, the majority of studies that assess the relation between verbal number knowledge and nonsymbolic quantity processing collapse across knower-level groups (Batchelor et al., 2015; Le Corre & Carey, 2007; Mix, 2008; Negen & Sarnecka, 2015; Sarnecka & Wright, 2013; Shusterman et al., 2017; Slusser et al., 2013). This solution may mask important differences within a heterogeneous group. Despite this, researchers have concluded that there is indeed a link between verbal number knowledge and nonsymbolic quantity processing, but it remains unknown whether it is learning individual verbal number words or acquiring knowledge of the cardinal principle that drives this link.

Regardless, the existence of the link between verbal number knowledge and nonsymbolic quantity processing has recently been questioned. Tightly controlled experimental studies indicate that verbal number word knowledge and nonsymbolic numerical abilities may be correlated because some experimental designs inadvertently allow children to correctly identify which of two arrays of two dots is more numerous by estimating the amount of surface area the dots take up rather than identifying the quantity of dots (Negen & Sarnecka, 2015; Rousselle, 2004). Indeed, the correlation between verbal number knowledge and nonsymbolic quantity processing disappears when the task includes a control that does not allow children to rely on cues from non-numerical magnitudes (such as the amount of surface area taken up by the dots) (Negen & Sarnecka, 2015). An example of a task that controls for non-numerical magnitudes in a task with nonsymbolic stimuli that includes conditions where a relatively smaller quantity of dots occupies a greater amount of surface area. In view of this, it is conceivable that non-numerical magnitudes, such as physical size, may be more salient features of sets than quantity for young children. In the current study, we aim to address the questions: 'do young children attend to quantity or size?' and 'does children's learning of number words affect whether children attend to number or size?'

Importantly, this finding, that forcing children to compare dots using quantity (rather than non-numerical cues) leads to chance performance across knower-levels, suggests that preschool-aged children may not yet have a clear concept of what 'quantity' is, and therefore may not understand the instruction to 'choose the side with more dots'. This is concerning because the vast majority of studies that have examined the link between verbal number knowledge and nonsymbolic number processing in young children have used tasks in which children are explicitly asked to compare quantities (e.g., Abreu-Mendoza et al., 2013; Batchelor et al., 2015; Dehaene, 2007; Gunderson et al., 2015; Le Corre & Carey, 2007; Mix, 1999, 2008; Mussolin, Nys, Leybaert, et al., 2014; Negen & Sarnecka, 2015; Shusterman et al., 2016, 2017; Slusser & Sarnecka, 2011; Slusser et al., 2013; Wagner & Johnson, 2011). A relatively smaller body of research has developed and used non-directive number tasks to assess individual differences in the degree to which children spontaneously focus their attention on quantities (SFON) (Baroody & Li, 2016; Baroody, Li, & Lai, 2008; Hannula & Lehtinen, 2005; Hannula, Räsänen, &

Lehtinen, 2007). In these studies, the term “spontaneous” refers to the idea that the process of focusing on quantity is un-cued by an experimenter and therefore self-initiated. The use of SFON-like paradigms overcomes a key limitation within this large body of literature, namely that experimenters cannot know for certain whether a child understands the instruction to choose the array with the greater numerosity. Additionally, SFON-style tasks have the advantage that it is possible to compare the degree to which children attend to quantity, to related dimensions (such as physical size). Consequently, the use of a SFON-like paradigm is ideal to assess 1) whether children spontaneously attend to quantity or physical size, and 2) evaluate whether verbal number knowledge affects the degree to which children attend to quantity vs. physical size.

5.1.3 The Current Study

Recent theories predict that acquiring verbal number knowledge may change the way children attend to discrete quantities in their environment (Barner, 2017; Merkley & Ansari, 2016), but this has not yet been tested empirically. Therefore, the goal of the current study is to investigate how number word knowledge relates to the way children spontaneously attend to number and size. To do so, we developed the train task, a task that can be used to investigate whether preschool-aged children attend to discrete quantity or physical size, without being cued to either. The train task is a SFON-like paradigm that requires a child to build a train that is the “same” as a train built by the experimenter. In the train task, the child and the experimenter have sets of blocks that differ in length. These blocks are used to build trains with varied numbers of cars. Therefore, the child is only able to make a train that matches the experimenter’s train based on either the number of cars or the length of the train, but not both. The train task was developed and used to measure whether children use a number strategy or a physical size strategy on a matching task when they are not explicitly cued to either strategy. The second question that the current study examines is how verbal number word knowledge relates to the use of number and size strategies on the train task. Examining the relation between verbal number knowledge and use of a number, compared to a size strategy on the train task, addresses the key question of whether having a symbolic referent in a child’s mind affects the degree to which he or she attends to number.

We anticipated four distinct possible outcomes for the way that children may respond to the train task. The first is that all children will use a number strategy, regardless of verbal number knowledge. This idea is supported by research suggesting that children are born with an innate number sense and automatically perceive discrete numerosity (Dehaene, 2007). In direct contrast is the prediction that all children will use a size strategy regardless of verbal number knowledge. This is supported by the notion that non-numerical magnitudes may be more salient to young children than discrete quantities (Henik, Leibovich, Naparstek, Diesendruck, & Rubinsten, 2011; Leibovich et al., 2017; Merkley, Thompson, & Scerif, 2016; Negen & Sarnecka, 2015; Szűcs, Nobes, Devine, Gabriel, & Gebuis, 2013). The third potential outcome is that CP-knowers will attend to number, whereas subset-knowers will attend either to size or neither number nor size. This is supported by research suggesting that the acquisition of the cardinal principle fundamentally changes the way that children process quantities (Abreu-Mendoza et al., 2013; Mussolin, Nys, Content, et al., 2014; Wagner & Johnson, 2011). Finally, it is possible that acquiring knowledge of each individual number word changes the way that children process that particular quantity. For example, a child who knows the meaning of the verbal number words one and two might use a number strategy for trains that have one or two cars, but not trains with three or more cars. This hypothesis is supported by data that suggests that knowing individual symbolic numbers relates to children's ability to attend to those numbers (Batchelor et al., 2015; Slusser & Sarnecka, 2011). In summary, this study uses a novel task to investigate the degree that children use number and size strategies during an un-cued matching task, and how the acquisition of verbal number words affect the degree to which children used these strategies.

5.2 Methods

5.2.1 Participants

One hundred forty children between the ages of 2-2 and 6-0 (years-months) were recruited to participate in this study. Of the 140 children whose parents consented for their child to participate, three children were excluded because they refused to participate, thirteen children were excluded due to failing at least one out of the two practice trials on the train task, four children were excluded because their parent or teacher explicitly told them to “count” or “use numbers” while completing the train task, and one child was excluded due to being the only pre-knower remaining in the sample. The final dataset consisted of 119 children ($Mean_{age}$ = 4.05, $SDev_{age}$ = 0.84; Females = 51, Males = 68; Age Range = 2-2-6-0 years). The non-medical research ethics board at the University of Western Ontario approved all procedures (See Appendix A). Written consent and assent were obtained from all legal guardians and children.

This sample size was based on an a priori power analysis, calculated using G*Power 3.1, for a split-plot three-way ANOVA examining the effect of knower-level, train length, and strategy type on the proportion of strategy use. The parameters used to calculate the required sample size include an effect size of 0.25, an alpha error probability of .05, and a power of 0.99. This a priori power analysis revealed that the required sample size was n=50 with a minimum of 10 participants per knower-level group (1-knower, 2-knower, 3-knower, 4-knower, CP-knower). One hundred and nineteen participants were collected as this was how many children were needed to ensure the smallest group (1-knowers) had ten usable participants.

5.2.2 Materials

5.2.2.1 The Train Task

The train task is a novel paradigm that measures whether children choose to use a number or a size strategy on a matching task when it is not possible to match on both. This task required a child to build a train that “matches” a train built by an experimenter. The task was played on a premade board, with a premade engine block leading the row of blocks for every example. The board contained two parallel train tracks with an engine at the front (see Figure 5.1A). There were three sizes of blocks for this task; small (3cm x 3cm x 4cm), medium (3cm x 3cm x 6cm) and large (3cm x 3cm x 9cm). All three block sizes were the same height and width. The small blocks were two thirds the length of the medium blocks and the medium blocks were two thirds the length of the large blocks (see Figure 5.1B). During the experiment, the child was given nine medium-sized blocks, and the experimenter had two medium-sized blocks, five small blocks, and five large blocks.

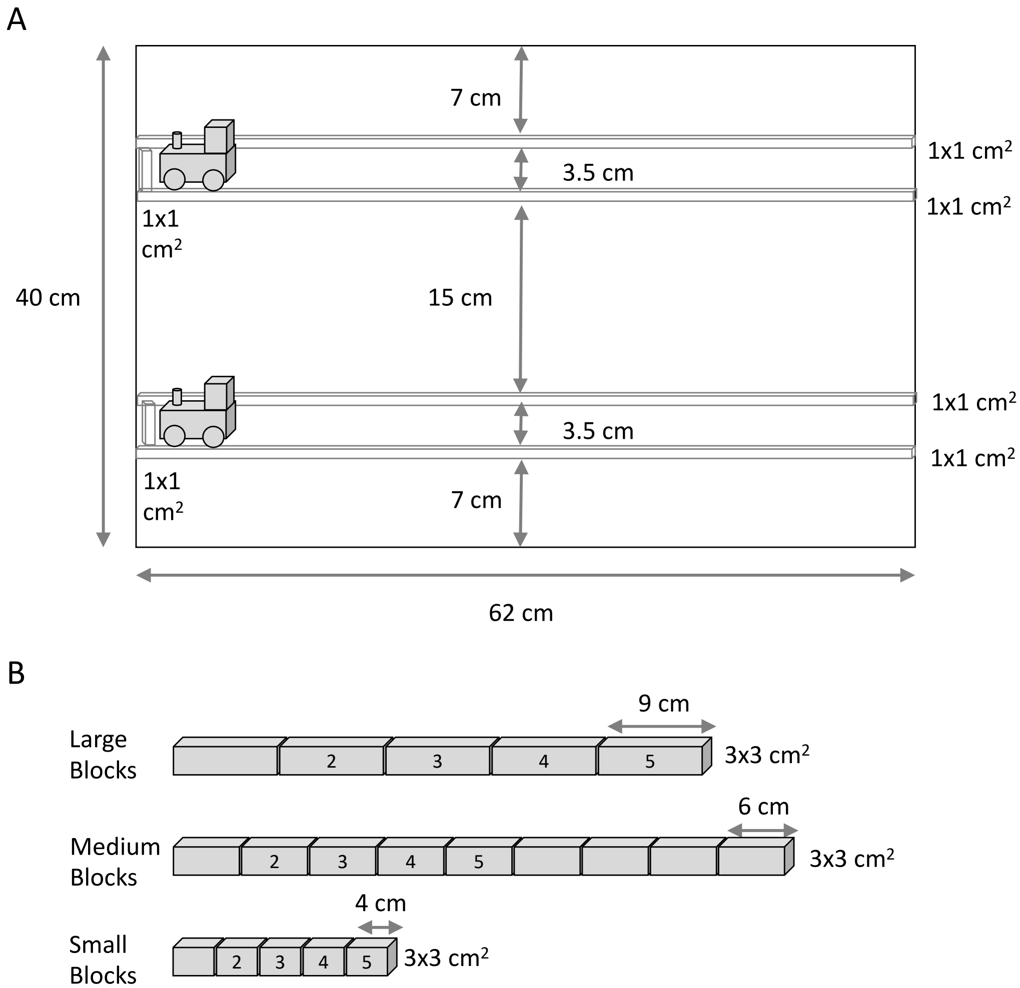

Figure 5.1 A) Dimensions of the board used for the train task. B) Dimensions of the three sizes of blocks used for the train task.

To begin the task, the experimenter built a train using two medium blocks on his or her own side of the board. The experimenter then said "I want you to make your train the same as mine. I will show you using your blocks." The experimenter used two of the child's medium blocks to build the same train (with two blocks behind the engine) on the child's side of the board. The child was then asked, "is your train the same as my train"? Once the child acknowledged that the experimenter's train and their train were the same, the experimenter conducted two practice trials. In the first practice trial, the experimenter built a train using a single medium block and said, "make your train the same as mine". The child then used his or her blocks to build a train with one block. If the child did not understand the instructions, the experimenter tried one or both of the phrases “make your train match mine,” or “make your train just like mine.” In the second practice trial, this was repeated using two medium blocks. Subsequently, the experimenter began experimental trials. Children who failed one or both practice trials (i.e., did not put one block down for the first practice trial and two blocks down for the second practice trial) completed the experimental trials but were excluded from analyses.

The experiment included 20 experimental trials. In each trial, the experimenter made a train using one to five blocks that were either all small blocks or all large blocks. The experimenter said, “make your train the same as mine.” The child tried to match their train to the experimenter’s, using their medium-sized blocks. The child completed the task by 1) making his or her train have the same number of blocks as the experimenter’s train (i.e., number strategy), 2) making his or her train the same length as the experimenter’s train (i.e., size strategy), or 3) making his or her train in a way that does not match on number or on length (i.e., incorrect). Once a child finished building each train, the experimenter confirmed that the child believed that the trains matched. The experimenter did not provide feedback and then began the next trial.

The 20 trials in the experiment were grouped into four blocks of five trials. Within a single block, the five trials included the experimenter building each of five different train lengths (one-five). Therefore, there were four trials (one in each block) for each of the five train lengths, meaning that a trial with each train length was built once in a block for a total of four times in the task. For train length one (i.e., building a train with a single block), the experimenter always used the large block. However, trials that include trains with a single block (i.e., train length 1) were excluded from analyses because it is not possible to tell whether a child is matching based on number or size for this train length. For all other train lengths (two-five), experimenters presented two trials using small blocks and two trials using large blocks. For example, a train made of four blocks was built twice using the small blocks and twice using the large blocks in a completed data set. There were four versions of the trial lists in which the order of blocks and the trials within the blocks were randomized. Children who completed fewer than 10 trials were excluded from analyses.

The following formula was used to compute a score to determine the normalized frequency of trials a child used a number strategy, and a size strategy for each train length (two to five).

1) $Normalized\ Frequency\ of\ Number\ Strategy =$

$$\left(\frac{Frequency\ of\ Number\ Strategy\ Used}{Total\ Number\ of\ Trials\ Completed}\right) \times$$

$$(Total\ number\ of\ trials\ in\ the\ condition\ of\ the\ experiment)$$

2) $Normalized\ Frequency\ of\ Size\ Strategy = \left(\frac{Frequency\ of\ Size\ Strategy\ Used}{Total\ Number\ of\ Trials\ Completed}\right) \times$

$$(Total\ number\ of\ trials\ in\ the\ condition\ of\ the\ experiment)$$

Below is an example of a calculation to compute the proportion that a child used a number strategy for train length of two if he or she completed all four trials and used a number strategy on two of the trials.

$$= \left(\frac{Frequency\ of\ Number\ Strategy\ Used\ for\ Train\ Length\ 2}{Total\ Number\ of\ Trials\ Completed\ for\ Train\ Length\ 2}\right)$$

$$\times\ (Total\ number\ of\ trials\ for\ train\ length\ 2\ in\ the\ experiment)$$

$$= \left(\frac{2}{4}\right) \times\ 4 = 2$$

Critically, if a child uses a number strategy for half of the trials, it does not mean that the child was at chance. For each trial, children have nine blocks with which to build their train. Therefore, the probability of a child using a number strategy by chance for a single trial is 1/9.

5.2.2.2 Give-a-Number Task

The give-a-number task (Give-N) is a widely used instrument that measures verbal symbolic number knowledge (Wynn, 1990). In the current study, the child was presented with 10 blocks and was asked to feed some number of these blocks to a finger puppet named Dino (who likes to eat blocks), by placing them on a plate. Typically, the experimenter says to the child, “can you feed Dino *n* blocks?” After the child finished placing the blocks on the plate the experimenter asked the child a single question: “is that *n* blocks?” If the child said no, the experimenter responded, “Dino really wants *n* blocks, can you make it *n*?" This is continued until the child confirmed that he or she believed *n* blocks to be on the plate. The experimenter initiated the trials by asking for one block. If the child was successful in feeding Dino one block, then the experimenter asked for three blocks. If the child was successful, the experimenter asked for one more block. If the child was unsuccessful, the experimenter asked for one fewer block. The experimenter increased or decreased the number of blocks in this way until the child correctly gave a certain number of blocks (*n* blocks) twice, and incorrectly $n + 1$ blocks twice. The knower-level of the child was inferred as the highest number that the child correctly gave twice. For example, a child who correctly fed Dino three blocks twice and incorrectly fed Dino when asked for four blocks twice was considered a three-knower. Children who correctly gave five or more blocks at least twice were considered cardinal-principle knowers.

5.2.3 Procedure

All participants were recruited through preschools, daycares, schools and family care centres in London, Ontario. The participants worked individually with an experimenter to complete the tasks. All participants first completed the train task to avoid any potential biases or priming of numbers that were present in the Give-N task. Participants were randomly assigned the trial order version for the train task. Following the completion of the train task, experimenters performed the Give-N task with the participant to assess knower-level of a child. The participants completed an additional two short assessments that were not analyzed for the current study. These two tasks included 1) children were asked to count as high as they could, and 2) children completed a basic instruction following task where the experimenter asked the children to touch their head or their toes eight times in a random order. The entire session took approximately 30 minutes. All participants received a certificate and stickers at the end of the testing session.

5.3 Results

The present study examined whether verbal symbolic number knowledge is related to the type of strategy used in the train task across four of the five different train lengths. Notably, for train length one, responding with a single block means that the participant and experimenter's trains matched in both size and number. Therefore, trials with train length "one" were excluded from all analyses. The give-N task was used to determine each participant's verbal symbolic number knowledge (i.e., knower-level). Of the 119 children who participated in the study, 10 children were one-knowers, 14 were two-knowers, 19 were three-knowers, 13 were four-knowers, and 63 were cardinal principle knowers (CP-knowers). The train task was used to determine the degree to which children spontaneously used a number strategy and size strategy. Each participant had 10 scores from the train task. Specifically, five scores were given for the proportion of a number strategy used for each of five train lengths, and five scores were given for the proportion of a size strategy used for each of five train lengths.

A three-way split-plot analysis of variance (ANOVA) was computed to examine how the proportion of number and size strategies used at different train lengths relates to knower-level. The within-subject variables were strategy (number vs. size) and train length (2 blocks, 3 blocks, 4 blocks, 5 blocks). The between-subject variable was knower-level (1-knower, 2-knower, 3-knower, 4-knower, CP-knower).

Levene's test of homogeneity of variance was performed on each level of the between-subjects factor to assess the equality of variances between the means of the groups. The Levene's test for the proportion of number used at train length three $F(4, 114) = 3.96$, $p = .005$, and four $F(4, 114) = 3.74$, $p = .007$ and proportion of size used at train length two $F(4, 114) = 4.44$, $p = .002$, were significant. The Levene's test of equality of variance for the proportion of number used at train lengths 2, and 5, and for the proportion of size used at train lengths 3, 4, and 5, were not significant. Mauchly's test of sphericity revealed that the current data violated the assumption of sphericity for both train-length, $W = .79$, $X^2 = 26.09$, $p = <001$, Greenhouse-Geisser = .89, and the interaction between strategy and train-length $W = .79$, $X^2 =26.73$, $p = <.001$, Greenhouse-Geisser = .86. Therefore, all subsequent analyses are reported using Greenhouse-Geisser adjusted values.

An examination of the main effect of strategy is used to distinguish between hypothesis 1 and 2, namely whether children are more likely to use a number strategy or a size strategy across train lengths and knower-levels. Results revealed a significant main effect of strategy, $F(1, 114) = 4.87$, $p = 0.03$, partial $\eta^2 = 0.04$, that indicated that children of all knower-levels used a number strategy (*Mean* = 1.53, *Standard Error* = 1.08) more often than they used a size strategy (*Mean* = 1.10, *Standard Error* = 0.10) across all train length trials (Figure 5.2). This supports the idea that in general children are more likely to use a number strategy over a size strategy.

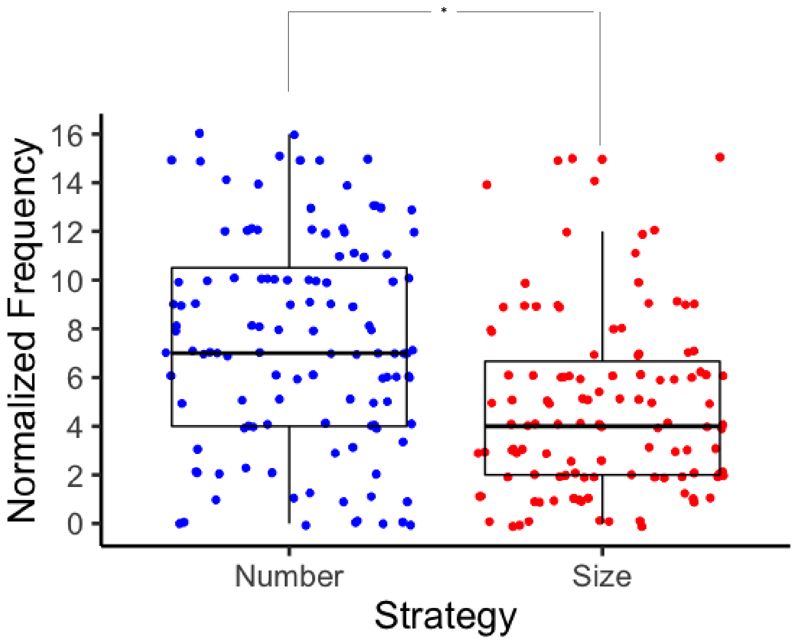

Figure 5.2 A) Main effect of strategy. Children use a number strategy significantly more than a size strategy *$p<.05$.

The two-way interaction examining whether the use of a number strategy over a size strategy is modulated by knower-level was used to measure whether verbal number knowledge related to strategy use (hypothesis 3). Results revealed that the interaction between strategy and knower-level was not significant $F(4, 114) = 1.55$, *ns*. This suggests that across train lengths, there is no effect of knower-level on strategy use.

Therefore, an examination of the three-way interaction was used to assess whether the use of a number strategy over a size strategy at different train lengths differs as a function of knowledge of each individual number word (hypothesis 3). The 3-way interaction between strategy, train length and knower-level was significant $F(10, 293) = 4.56$, $p = <.001$, $\eta2 = 0.138$, (Figure 5.3). This finding reveals that train length influenced whether children were more likely to use a number strategy or a size strategy differently at each knower-level. Post-hoc pairwise comparisons with a Bonferroni correction for multiple comparisons were included to examine simple main effects. For one-knowers, there was no significant difference between the use of a number strategy and length strategy at any train length. Two-knowers used a number strategy more than a size strategy for train length two ($p = .001$), but there was no significant difference for train lengths three, or four. Two-knowers used a size strategy more than a number strategy for train length five ($p = 0.018$). Three-knowers used a number strategy more than a size strategy at train lengths two ($p <.001$), and three ($p = .008$) but there was no significant difference in strategy use for train length four or five. Four-knowers also used a number strategy more than a size strategy at train lengths two ($p <.001$), and three ($p = .024$), but not train length four. Four-knowers used a size strategy significantly more than a number strategy for train length five ($p < .001$). CP-knowers used a number strategy more than a size strategy at train lengths two ($p < .001$), and three ($p < .001$). There was no significant difference in strategy use for CP-knowers on train length four. CP-knowers used a size strategy significantly more than a number strategy for train length five ($p < .001$). These results suggest that children who are one-knowers, two-knowers and three-knowers were more likely to use a number strategy for train lengths within their knower-level. Additionally, all children except 1-knowers and 3-knowers used a size strategy significantly more than a number strategy for train length five. Notably, four-knowers and CP-knowers displayed similar patterns of strategy use to three-knowers in that they were more likely to use a number strategy than a size strategy for train lengths two and three.

Therefore, this significant three-way interaction indicates that acquiring knowledge of each individual number word changes the way that a child processes that particular number, particularly for small numbers (two and three). For example, two-knowers are more likely to use a number strategy for trains that have two blocks but not trains with three or more blocks.

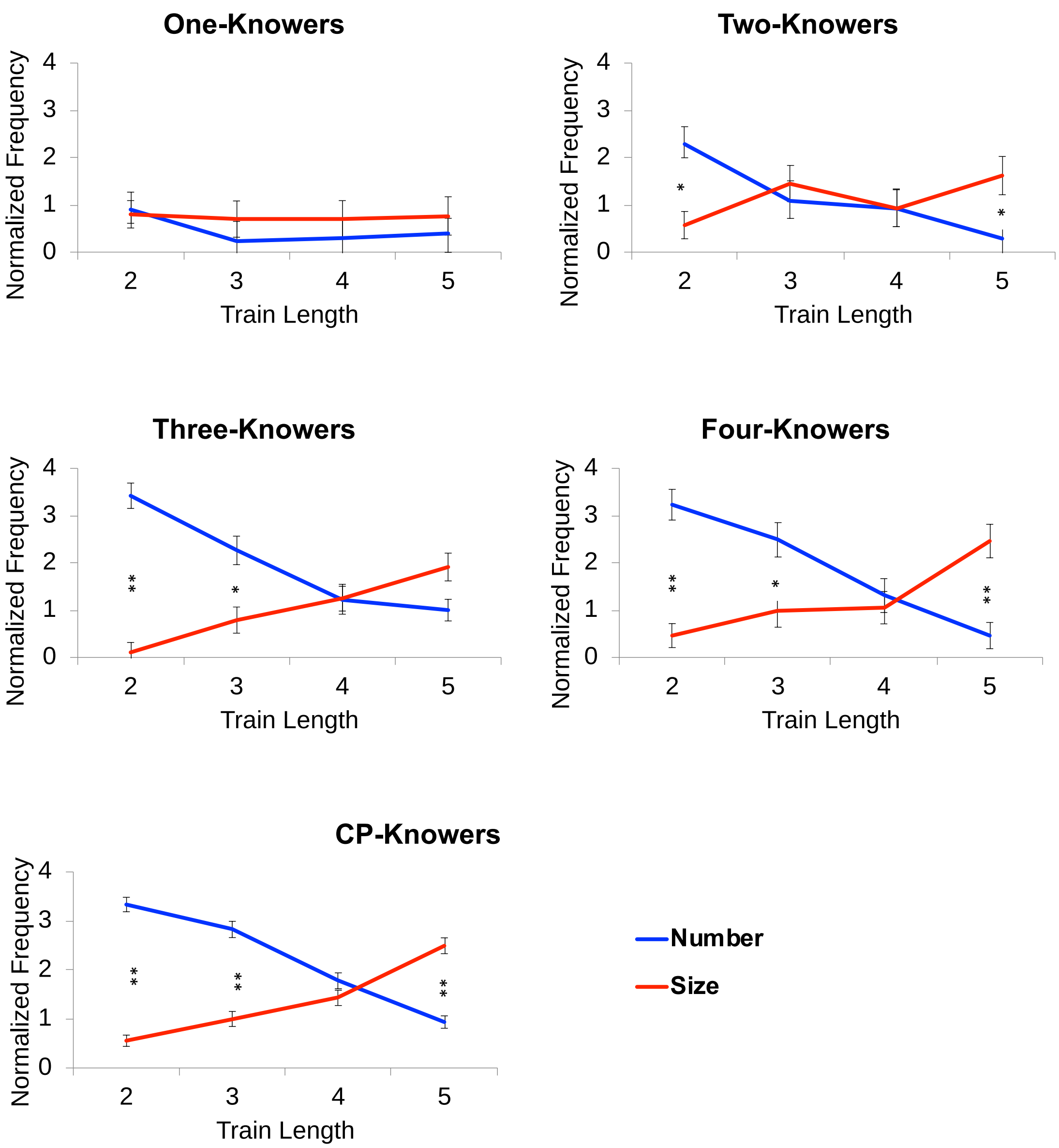

Figure 5.3 Three-way interaction of strategy by knower-level by train-length. Children are more likely to use a number strategy when building a train where the length of the train is within their knower-level. *p<.05, **p<.001.

There were several main effects and two-way interactions that did not correspond to the hypotheses presented in the introduction but are reported here for completeness. Specifically, there was a significant main effect of knower-level, $F(4, 114) = 29.30$, p =

$<.001$, partial $\eta^2 = 0.51$, which showed that use of a strategy (number or size) increased as knower-level increased. The main effect for the length of train was also significant $F(3, 305) = 28.24$, $p <.001$, partial $\eta^2 = 0.20$, revealing that the use of any strategy (number and size) decreased as train lengths increased. The two-way interaction between train length and knower-level was not significant $F(11, 275) = 1.33$, *ns*, indicating that there is no difference in the degree to which children use either strategy (number or size) across train lengths and between knower-levels. Finally, the two-way interaction between strategy and train length was significant $F(3, 293) = 68.29$, $p <.001$, partial $\eta^2 = 0.38$, revealing that the use of a number strategy compared to a size strategy differed depending on the length of the train being built across all children. Post-hoc pairwise comparisons with a Bonferroni correction for multiple comparisons revealed that children used a number strategy significantly more than a size strategy for train length 2 ($p <.001$), and 3 ($p = .001$). There was no difference in the use of a number vs. a size strategy for train length 4. Children used a size strategy significantly more than a number strategy for train length 5 ($p <.001$) (Figure 5.4). This finding suggests that children's strategy use is dependent on the length of the train they are matching, across all knower-levels.

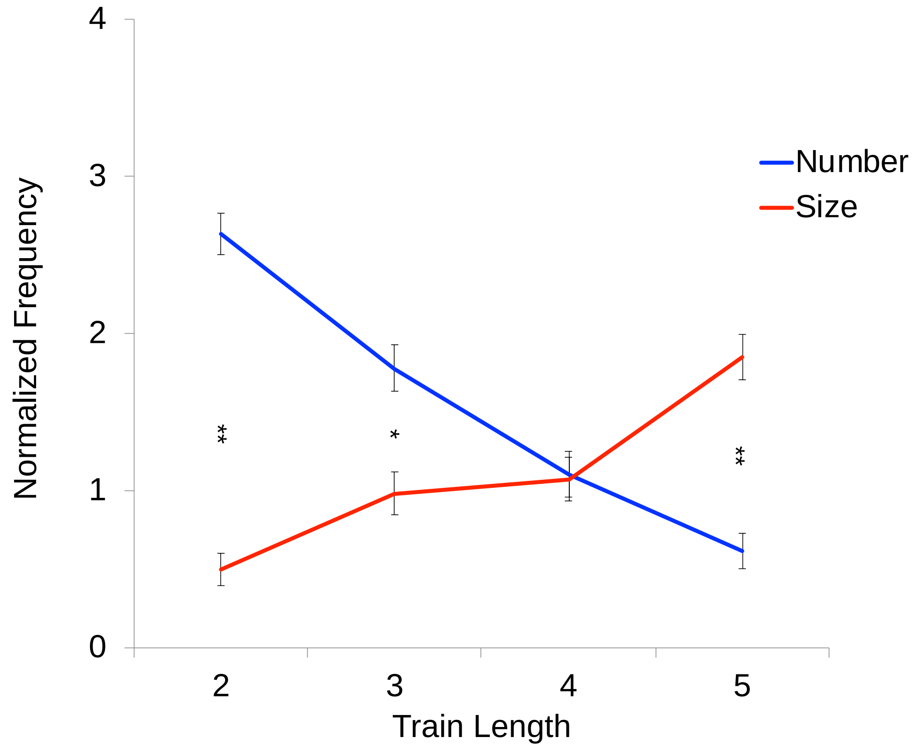

Figure 5.4 Two-way interaction of strategy by train-length. Children are more likely to use a number strategy when building a train with a length of two or three blocks. Children and are more likely to use a size strategy when building a train with a length of five blocks. *p<.05, **p<.001.

As knower-level is often correlated with age, an additional control analysis was computed to determine whether the effects from the previous analysis were driven by knower-level and not by age. A three-way split-plot analysis of covariance (ANCOVA) was computed to examine how the proportion of number and size strategies used at different train lengths relates to knower-level while controlling for age. The within and between-subject variables were the same as the ANOVA reported above for strategy (number vs. size), train length (2 blocks, 3 blocks, 4 blocks, 5 blocks), and knower-level (1-knower, 2-knower, 3-knower, 4-knower, CP-knower). The covariate was age. Results from this control analysis revealed that all effects from the original three-way split-plot ANOVA were unchanged when age was included as a covariate.

In sum, the results from experiment 1 support those proposed in outcome four, namely that learning verbal number words changes the way that children engage with numerical quantities in the environment, but only for small quantities (i.e., train length two and three). For trains with five cars, most participants used a size strategy more than a number strategy.

5.4 Discussion

The current study examined a) whether children attend to number or physical size when not explicitly cued to either and b) whether verbal number knowledge influences strategy choice on a novel matching task. In view of previous research, we anticipated four distinct potential outcomes for how children would respond to the train task. First, as supported by research suggesting that children are born with an innate number sense (e.g., Dehaene, 2007), it was possible that all children would use a number strategy, regardless of verbal number knowledge. In direct contrast, research highlighting the salience of continuous magnitudes to young children (e.g., Leibovich et al., 2017) supports the outcome that all children would use a size strategy, regardless of verbal number knowledge. It was also possible that children who have acquired the cardinal principle would attend to number, whereas children who have not yet acquired the cardinal principle would attend either to size or neither number nor size. Indeed, this prediction was supported by the replicable finding that the acquisition of the cardinal principle fundamentally changes the way that children process quantities (Abreu-Mendoza et al., 2013; Mussolin, Nys, Content, et al., 2014; Wagner & Johnson, 2011). Our fourth and final anticipated outcome was that verbal number knowledge of each individual number word would change how a child processed that particular quantity.

Results broadly aligned with outcome one, namely, that children used a number strategy more than a size strategy (with the exception of trains with five cars, where children used a size strategy more than a number strategy). However, the degree to which children used a number strategy more than a size strategy increased as a function of children’s knowledge of the cardinality of the count word that corresponded to the number of blocks in the train that they were instructed to match, specifically for small quantities. This suggests that, as proposed in outcome four, learning verbal number words that correspond to small quantities changes the way that children engage with numerical quantities in the environment. Specifically, number symbols may be a tool for guiding children's behaviour on a task in which number and size are in conflict.

5.4.1 Learning Verbal Number Words Changes Attention and Behaviour

Although there is a main effect demonstrating that children use a number strategy more than a size strategy to complete the train task, this effect is further modulated by the individual child's number word knowledge. In particular, children's use of a number strategy over a size strategy increased as knower-level increased, particularly for small numbers (i.e., quantities two and three). This highlights that greater knowledge of verbal number words corresponds to greater use of a number strategy, particularly for small numbers. The current study uses a SFON-like task to examine the effect of verbal number knowledge on spontaneously attending to numerical quantities. Previous research has shown that children's verbal number knowledge relates to explicit nonsymbolic number processing abilities (e.g., Le Corre & Carey, 2007; Mix, 1999, 2008). Indeed, when explicitly cued, subset-knowers (i.e., children with some verbal number word knowledge, but who have not yet learned the cardinal principle), can map small numbers (e.g., 1-4) to quantities (Le Corre & Carey, 2007). Relatedly, subset-knowers were able to make magnitude comparisons between dot arrays and verbal number words if they understood the meaning of those verbal number words (Batchelor, Keeble, et al., 2015). Subset-knowers can also successfully judge numerical equivalence of small quantities (Mix, 1999, 2008), and have some basic understanding that number words pertain to discrete, but not continuous quantities (Slusser et al., 2013). This research suggests that children can link small number words to the quantities before they have acquired the cardinal principle. The present findings build on this research, to evaluate whether children who *can* link verbal number words to quantities actually *use* this knowledge in a non-directed task.

Findings from the SFON literature reveal that spontaneously attending to quantities correlates with symbolic number abilities. Specifically, individual differences in SFON predict counting ability (Hannula et al., 2007) as well as subsequent mathematical knowledge (Batchelor, Inglis, & Gilmore, 2015; Hannula & Lehtinen, 2005; Nanu, McMullen, Munck, Hannula-Sormunen, & Hannula-Sormunen, 2018). Critically, previous SFON research has assessed counting using measures of procedural abilities. Moreover, while previous SFON studies include dimensions aside from number (such as colour or shape), these dimensions are not inherently correlated with quantity processing like size. By using a SFON-like task where participants can use number or size, and including a measure of conceptual verbal number knowledge, rather than procedural verbal number knowledge, we discovered that children who have verbal number knowledge, *choose* to use a strategy that relies on this knowledge for small numbers. This finding suggests that children use their number word knowledge even when they have not been cued to use it and when there is another strategy (size) available to solve the problem. Specifically, the findings revealed that one-knowers, two-knowers and three-knowers are more likely to use a number strategy than a size strategy if the child knows the verbal number word that corresponds to the number of blocks in the train. For example, a two-knower was more likely to use a number strategy than a size strategy for trains with one block or two blocks, but not for trains with three, four or five blocks. However, This finding significantly extends previous research that has highlighted that children *can* link quantities to verbal number words for which they have learned the meaning (Batchelor, Keeble, et al., 2015). Specifically, the present data reveal that children are more likely to use a number strategy when building a train where the length of the train is within their knower level.

As previously discussed, the null finding that children do not use a number strategy for trains with quantities above their knower-level does not necessarily mean that children are unable to process quantities for which they do not yet know the label. In other words, the current data cannot speak to whether children perceive number. Indeed, it has been reported that infants have the ability to track one to three objects using the parallel individuation (PI) system (Feigenson & Carey, 2003, 2005; Xu, 2003). This data suggests that preschool-aged children who do not yet know their number words could complete the task by matching quantity using the PI system, but they do not do so. The current study measured children's behaviour, and specifically, the frequency with which children use number to guide their behaviour. Consequently, the term 'attends', in this context, refers to the degree to which children use a number strategy. Therefore, the results from the current study align with outcome four to suggest that the acquisition of a semantic label (i.e., a verbal number word) strengthens the degree to which a child accesses and uses their conceptual knowledge of exact quantity to guide their behaviour in a situation that does not explicitly require them to integrate that knowledge into their behaviour.

5.4.2 Acquisition of the Cardinal Principle

The third potential outcome predicted for the current study was that children who have acquired the cardinal principle would attend to number, whereas children who have not yet acquired the cardinal principle would attend either to size or neither number nor size. This hypothesis is supported by research suggesting that the acquisition of the cardinal principle fundamentally changes the way that children process quantities (Abreu-Mendoza et al., 2013; Mussolin, Nys, Content, et al., 2014; Slusser & Sarnecka, 2011; Wagner & Johnson, 2011). For example, ability to approximately estimate which of two quantities has more dots on an 'approximate number task' has been linked to the acquisition of the cardinal principle (Mussolin, Nys, Content, et al., 2014; Wagner & Johnson, 2011). Knowledge of the cardinal principle has also been associated with children's ability to be fair (i.e., share equally) (Chernyak, Harris, & Cordes, 2018) and successfully extend number words from one set to another based on quantity. This body of research suggests that the acquisition of the cardinal principle fundamentally changes the way children conceptualize quantities. Results from the current study conflict with this conclusion. Indeed, our findings suggest that it is not becoming a cardinal principle-knower that changes the way children attend to quantity, but instead, learning individual numbers (i.e., shifting from a 1-knower to a 2-knower) relates to changes in the way children approach the train task. Moreover, children who know some numbers (e.g., four-knowers) but have not yet acquired the cardinal principle, produce a pattern of results that aligns more closely with CP-knowers than children who are just beginning to learn number words (i.e., one-knowers). Thus, the current study indicates that it is the process of acquiring labels for representations of quantities (i.e., verbal number words), rather than acquiring knowledge of the cardinal principle, that relates to changes the way that children attend to quantity in the absence of explicit cues.

Many previous studies that examined verbal number knowledge had small sample sizes in each knower-level group (Batchelor, Keeble, et al., 2015; Le Corre & Carey, 2007; Mix, 2008; Negen & Sarnecka, 2015; Sarnecka & Carey, 2008; Sarnecka & Wright, 2013; Shusterman et al., 2017, 2016; Wagner & Johnson, 2011). To overcome power issues, researchers grouped together knower-level groups in several small groups (e.g., 1 and 2-knowers vs. 3 and 4-knowers) (Batchelor et al., 2015; Le Corre & Carey, 2007; Sarnecka & Carey, 2008) or one large group (i.e., subset-knowers vs. CP-knowers) (Mix, 2008; Negen & Sarnecka, 2015; Sarnecka & Wright, 2013; Shusterman et al., 2017) for statistical analyses. Results from the current study highlight that learning each verbal number word influences the way that children attend to quantities. This indicates that a group of “subset-knowers” is a heterogeneous group. In view of this, future research that explores differences between knower-level groups should acquire a large enough sample size to analyze each knower-level group separately.

5.4.3 Two-Systems of Nonsymbolic Cognition

When examining the patterns of results from the current study, it is important to note that most children use a size strategy more than a number strategy on trains with five blocks. Indeed, the complete pattern of results from the current study reveal that children use a number strategy more than a size strategy for small quantities (i.e., up to three) if they know the corresponding verbal number word, number and size strategies are used equally frequently for trains with four blocks, and a size strategy is used more than a number strategy on trains with five blocks.

A possible explanation for why children might consistently be using a size strategy more than a number strategy for trains with longer lengths (i.e., five blocks), is that children may be using two distinct systems to process small and large train lengths. It has been suggested that humans have two systems that represent nonsymbolic quantities (for review see, Hyde, 2011). These systems include 1) the parallel individuation system (PI), used to track objects in order to process the exact amount of small sets of objects (i.e., quantities of one-four), and 2) the approximate number system (ANS), which uses approximate estimation to process larger quantities (i.e., quantities greater than four). Here we speculate that perhaps children are more likely to use a number strategy for trains with a small number of cars because they can track the exact number of cars in the train using parallel individuation. In contrast, a size strategy is perhaps the more salient strategy for trains with a greater number of blocks because these trains are processed using approximate estimation. Indeed, as trains with larger lengths have more items than can be processed using the PI system, the quantity of blocks in the trains can be processed using either automatic estimation or effortful counting. Therefore, we speculate that perhaps CP-knowers do not use a number strategy for long train lengths because an approximate size-based strategy aligns more closely with the system used to process the train.

5.4.4 Flexibility of Strategy

The finding that CP-knowers use a size strategy for trains with five cars, even when they know the verbal number word for five aligns with a related body of work that reveals that young children are more exploratory in their behaviour than are adults (Gopnik, 1996; Gopnik, Griffiths, & Lucas, 2015; Gopnik et al., 2017; Gopnik & Wellman, 2012; Plebanek & Sloutsky, 2017). Younger children outperform older children on learning tasks such as remembering information that the experimenter did not cue the participant to attend to, (Plebanek & Sloutsky, 2017; Sloutsky & Fisher, 2004) and learning atypical abstract causal principles from patterns of evidence (Gopnik et al., 2015). Authors of these studies have suggested that younger minds are intrinsically more flexible, and consequently more exploratory. It is perhaps for this reason that data from the current study revealed that children use a size strategy for a particular trial type when they likely have the ability to use a number strategy for that trial type.

In view of this, it is logical that children who know their verbal number words will be able to flexibly switch between a number strategy and size strategy, depending on which strategy is optimal to solve the problem. We discuss above that a number strategy may be more challenging to use for trains with five cars, as quantities with five or more objects are supported by the ANS, rather than the PI system. However, a size strategy may also be a less cognitively demanding strategy to solve the problem for trains with five cars because trains number and size are correlated. This means that, in order to match a train on quantity, the participant must inhibit the fact that the two trains are different lengths and trains with more cars differ more in length. Critically, size has been reported to influence attention even when it is the irrelevant dimension (i.e., when participants are told to ignore the size of an object) (Henik & Tzelgov, 1982; Henik, Gliksman, Kallai, & Leibovich, 2017; Leibovich, Diesendruck, Rubinsten, & Henik, 2013). In the train task, although the size of the child's individual blocks consistently differs from the experimenter's blocks at a ratio of 2 cm to 3 cm, the absolute length of the train is inherently related to the number of blocks included in the train (Leibovich & Henik, 2013). For example, in a trial where the experimenter uses large blocks (length 9 cm) and the child uses medium blocks (length 6cm), the absolute length of a train with two blocks would be 12 cm for the child and 18 cm for the experimenter (i.e., the absolute length difference is 6 cm). In contrast, if the experimenter uses large blocks (length 9 cm) and the child uses medium blocks (length 6cm) to build a train with five blocks, the absolute length of the child's train would be 30 cm and the absolute length of the experimenter's train would be 45 cm (i.e., the absolute length difference is 15 cm). Therefore, to match based on number requires a child to inhibit the difference of the absolute length of the two trains to a greater degree for trains with more blocks. In view of this, it is conceivable that on trials with more blocks, less effort is required for a child to use a size strategy compared to inhibiting the absolute length difference between the two cars, in order to use a number strategy.

The key pattern of results from the current study (that children are more likely to use a number strategy if they know the verbal number word corresponding to the train length) is driven by one-knowers, two-knowers, and three-knowers. Four-knowers and CP-knowers produce the same pattern of results as three-knowers. A potential explanation for this finding is that children flexibly shift to a size strategy on trains with four or five blocks to avoid the challenging task of inhibiting absolute length. Critically, future research should examine whether adjusting the absolute length of the trains, for those with more blocks, affects whether children use a number or a size strategy.

5.4.5 Conclusions

Learning the meaning of verbal number words is a slow process that sets a critical foundation for young children's numerical thinking. The key finding of the current study is that preschool-aged children were more likely to use a number strategy than a size strategy if they knew the verbal number word that corresponded to the number of cars comprising the train they were asked to match, particularly for small numbers. Results also revealed that children are more likely to use a size strategy than a number strategy for trains with five cars. Together, this study revealed that acquiring verbal number word knowledge may fundamentally affect the way that young children attend to quantities. In summary, this research provides a concrete example of how learning symbols influence behaviour within the domain of early number processing.

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Chapter 6

6 General Discussion

The capacity to estimate and discriminate between nonsymbolic numerical magnitudes (e.g., the number of objects in a set) emerges early in development and is shared with non-human species (Cantlon, 2012; Dehaene, 2007; Dehaene et al., 1998; Nieder & Miller, 2004). Consequently, this ability to represent and process nonsymbolic numerical magnitudes is assumed to be evolutionarily ancient and biologically endowed. In contrast, the uniquely human capacity to process numbers symbolically has emerged relatively recently in human history and is acquired through enculturation (Ansari, 2008; Coolidge & Overmann, 2012). The ability to conceptualize and use symbolic numbers is a necessary foundation for higher-level mathematical thinking, which is essential to a successful society (Bynner & Parsons, 1996; Duncan et al., 2007; Romano et al., 2010). The culturally mediated process of learning symbolic numbers is thought to be rooted in a pre-existing, innate and evolutionarily ancient abstract number processing system that evolved to process nonsymbolic numerical magnitudes (Brannon, 2006; Dehaene, 2007; Dehaene et al., 2003; Nieder & Dehaene, 2009).

However, a growing body of recent evidence suggests that systems used to process symbolic and nonsymbolic numerical magnitudes may be more distinct than previously assumed (Ansari, 2007; Bulthé, De Smedt, & Op de Beeck, 2014; Cohen Kadosh & Walsh, 2009; Lyons, Ansari, & Beilock, 2012, 2014; Lyons & Beilock, 2013; Sokolowski & Ansari, 2016). These data conflict with the notion that numbers are processed entirely abstractly. Despite years of research, the question of whether symbolic numerical magnitudes are processed using the evolutionarily ancient system that evolved to process nonsymbolic numerical magnitudes remains unanswered. To address this question, this thesis examined the relationship between symbolic and nonsymbolic numerical magnitude processing at the neural level in human adults. Additionally, this thesis explored how symbolic and nonsymbolic numerical magnitude processing is influenced by the participant's attentional state, and how the relationship between symbolic and nonsymbolic numerical magnitude processing changes across developmental time. In the following sections, I will discuss the results of the four empirical chapters presented in this thesis and relate these findings to other data and theories in the field. Following this, I will discuss the general limitations of these studies, implications of the findings, and future directions.

6.1 The Neural Correlates of Symbolic and Nonsymbolic Numerical Magnitude Processing

In recent years, there has been substantial growth in neuroimaging studies investigating the neural correlates of symbolic (e.g., Arabic numerals) and nonsymbolic (e.g., dot arrays) numerical magnitude processing. At present, it remains contested whether numbers are represented abstractly, or if number representations in the human brain are format-dependent (for review see: Cohen Kadosh, 2008). In chapter 2 of the current thesis (Sokolowski, Fias, Mousa, & Ansari, 2017), I used activation likelihood estimation (ALE) to conduct the first quantitative meta-analysis to synthesize all neuroimaging papers that examined symbolic and/or nonsymbolic numerical magnitude processing in the human adult brain. Results of this empirical chapter revealed that across all neuroimaging papers there are convergent areas of activation that are common to symbolic and nonsymbolic numerical magnitude processing. More specifically, conjunction analyses intended to quantify brain regions that supported both symbolic and nonsymbolic numerical magnitude processing revealed overlapping activation for symbolic and nonsymbolic numerical magnitude processing in regions along the frontal and parietal lobes. This finding of overlapping activation for symbolic and nonsymbolic numerical magnitude processing is consistent with the idea that there are regions in the human brain that process numerical magnitudes abstractly (Cantlon, 2012; Dehaene, 2007; Dehaene et al., 1998; Piazza et al., 2007). However, there were also brain regions that were specifically associated with either symbolic *or* with nonsymbolic numerical magnitude processing. Specifically, contrast analyses revealed anatomically distinct frontoparietal activation associated with symbolic and with nonsymbolic numerical magnitude processing. These findings that symbolic and nonsymbolic numerical magnitudes are supported by distinct brain regions are consistent with the notion that regions within the human brain processes numbers in a format-dependent way (Bulthé et al., 2014; Cohen Kadosh, 2008; Holloway et al., 2010; Lyons et al., 2014; Lyons &

Beilock, 2013; Sokolowski & Ansari, 2016). Specifically, these contrast analyses revealed that the representations supporting symbolic and nonsymbolic numerical magnitudes may be lateralized within the partial cortex. Indeed, the meta-analysis reported in chapter 2, implicated the left angular gyrus as potentially important for supporting symbolic numerical magnitude processing, whereas the right superior parietal lobule may be important for processing nonsymbolic numerical magnitudes (Sokolowski et al., 2017). Unsurprisingly, this finding of lateralization of symbolic compared to nonsymbolic numerical magnitudes in the parietal cortex at the meta-analytic level aligns with findings reported in many individual empirical studies (For review see: Sokolowski and Ansari, 2016). Together, data from this chapter reveals that symbolic and nonsymbolic numerical magnitudes are sub-served by both format-dependent and abstract neural systems, thus suggesting that some components of the evolutionarily ancient system used to process nonsymbolic magnitudes may be repurposed for the processing of symbols. However, due to several key inherent methodological limitations of meta-analyses that are discussed in the following paragraph, even the findings of overlapping activation for symbolic and nonsymbolic numerical magnitudes, reported in chapter 2, cannot be used to conclude that symbolic and nonsymbolic numerical magnitudes are processed in the same way, using a single evolutionarily ancient system.

The use of ALE methodology in chapter 2 is valuable because the algorithm can be used to extract regularities across a large set of empirical studies with vastly different methodologies. However, when using meta-analytic techniques, it is challenging to account for differences in statistical thresholding, spatial extent, and magnitude of activations across regions of activation both within and between studies (Arsalidou & Taylor, 2011; Christ et al., 2009; Di Martino et al., 2009; Ellison-Wright et al., 2008). Additionally, there are many limitations within the empirical studies that comprise the meta-analysis in chapter 2. For example, the majority of the studies included in the meta-analysis 1) did not adequately control for non-numerical magnitudes and 2) used active task designs. The lack of control for non-numerical magnitude processing means that the system being examined, that is assumed to be an abstract number processing system, may, in fact, be a general magnitude processing system used to processing both numerical and non-numerical magnitudes (Cantlon, Platt, & Brannon, 2009; Sokolowski, Fias, Ononye, & Ansari, 2017; Van Opstal & Verguts, 2013; Walsh, 2003). Relatedly, the use of these active tasks makes it impossible to conclude whether the overlapping brain regions that support symbolic and nonsymbolic numerical magnitudes is a consequence of abstractly processing the magnitude or if this overlapping activation relates to decision making, motor processing or task difficulty (Göbel et al., 2004). In view of these limitations, it was critical to identify the neural correlates of symbolic and nonsymbolic numerical magnitude processing in a single set of participants using a paradigm that controls for non-numerical magnitude processing and activations associated with active tasks.

In chapter 3 of the current thesis, I presented data from an experimental fMRI study in which I assessed whether symbolic and nonsymbolic numerical magnitude processing is supported by overlapping neural activation when controlling for confounds associated with active tasks and non-numerical magnitudes. Specifically, I developed and used an fMRI adaptation paradigm that isolated the representations of symbolic numerical magnitudes, nonsymbolic numerical magnitudes, and physical size (a non-numerical magnitude), in forty-five human adults. Results from this chapter indicated that the neural correlates associated with the passive viewing of numerical symbols were distinct from the neural correlates that were associated with the passive viewing of nonsymbolic numerical magnitudes and physical size. Surprisingly, no brain region was significantly activated by the passive viewing of *both* symbolic and nonsymbolic numerical magnitudes. Passive processing of symbolic numerical magnitudes correlated with activation in the left superior parietal lobule, whereas the processing of both nonsymbolic numerical magnitudes and physical size correlated with activation in the right intraparietal sulcus. This finding aligns with results from chapter 2 as well as previous research that reports hemispheric lateralization of symbolic and nonsymbolic numerical magnitude processing within the parietal cortex. Data from chapter 3 also provide novel evidence to suggest that the overlapping brain regions that support symbolic and nonsymbolic numerical magnitude processing, reported in chapter 2, as well as previous studies (e.g., Dehaene et al., 1998; Dehaene, 2007; Cohen Kadosh, 2008; Sokolowski and Ansari, 2016), may be due to overlapping task demands, and consequently may not be indicative of an abstract number processing region. Notably, results from chapter 3 also revealed that symbolic and nonsymbolic numerical magnitudes are distinct at the representational level, in addition to spatially. Specifically, representational similarity analyses (RSA) were conducted within regions of interest derived from regions that exhibited overlapping activation for symbolic and nonsymbolic numerical magnitude processing in chapter 2. These RSA analyses revealed that the passive processing symbolic numerical magnitudes exhibited dissimilar normalized patterns of activation compared to the passive processing of nonsymbolic numerical magnitudes in the regions of interest in both the left and right parietal lobes. Notably, the patterns of activation associated with nonsymbolic numerical magnitudes and were practically indistinguishable from the patterns of activation associated with the non-numerical magnitude, physical size. Therefore, the results from chapter 3 suggest the system used to process symbolic numerical magnitudes are quite distinct from the system that is used to process nonsymbolic numerical magnitudes in human adults. Additionally, these results provide evidence in support of the idea that the evolutionarily ancient system used to process nonsymbolic numerical magnitudes may be a general magnitude processing system rather than a specific abstract number processing system (For other research supporting the idea that numbers are processed using a general magnitude system see: Cantlon, Platt, et al., 2009; Cohen Kadosh et al., 2008; Sokolowski, Fias, Bosah Ononye, et al., 2017; Walsh, 2003).

In summary, the results from chapter 2, revealed overlapping and distinct regions of activation for symbolic and nonsymbolic numerical magnitude processing when extracting regularities across a large set of attentional task demands. However, using a paradigm that removed confounds associated with active task demands (i.e., chapter 3) revealed that symbolic and nonsymbolic numerical magnitude processing may be even more distinct than previously assumed. These findings challenge the longstanding belief that the culturally acquired ability to conceptualize symbolic numbers is rooted in an evolutionarily ancient system that evolved to support nonsymbolic numerical magnitude processing. Moreover, these data revealed that the system used to process nonsymbolic numerical magnitudes may actually be a general magnitude processing system used to process nonsymbolic numerical magnitudes and non-numerical magnitudes.

6.2 Attentional Conditions Affect the Processing of Symbolic and Nonsymbolic Numerical Magnitudes

Although the two methodologies reported in chapter 2 and chapter 3 are useful for developing our understanding of the way the human brain represents symbolic and nonsymbolic numerical magnitudes across multiple methodologies, and in the absence of task demands, they do not identify how different attentional conditions affect symbolic and nonsymbolic numerical magnitude processing. Key findings from research exploring symbolic and nonsymbolic numerical magnitude processing reveal that although both symbolic and nonsymbolic magnitudes *can* be processed automatically, whether or not they *are* processed automatically depends upon their relevance to the task at hand (Furman & Rubinsten, 2012; Naparstek & Henik, 2010, 2012; Naparstek et al., 2015; Pansky & Algom, 2002). In other words, the degree to which a task requires a participant to attend to a symbolic and a nonsymbolic numerical magnitude affects the processing of the stimuli. In Chapter 4 of the current thesis, I explore the degree to which symbolic compared to nonsymbolic numerical magnitude processing is influenced by attentional demands of the task.

In chapter 4, I developed and used a Stroop-like paradigm to assesses the effortful and the automatic processing of symbolic numerical magnitudes compared to nonsymbolic numerical magnitudes. In this paradigm, participants (N_{Study1} = 80, N_{Study2} = 63) compared adjacent arrays of number symbols (e.g., 4444 vs 333). Participants were instructed to indicate which side contained *either* the greater quantity of symbols (nonsymbolic task) or the numerically larger symbol (symbolic task). This manipulation allowed for both symbolic and nonsymbolic numerical magnitudes to act as the relevant dimension and the irrelevant dimension. The aspect of the stimulus that the participant was instructed to focus on was considered the relevant dimension and was used to assess effortful processing, whereas the aspect of the stimulus that participant could ignore when making the comparison was referred to as the irrelevant dimension and was used as a measure of automatic processing. Results revealed that the effortful processing of symbolic numerical magnitudes is more efficient (i.e., faster and more accurate) and less affected by numerical distance than the effortful processing of nonsymbolic numerical magnitudes. These results converge with findings from previous research that examined the effortful processing of symbolic compared to nonsymbolic numerical magnitudes using tasks that did not include an irrelevant dimension Holloway & Ansari, 2009; Holloway et al., 2010; Lyons & Ansari, 2009; Moyer & Landauer, 1967). Results from chapter 4 also provided novel evidence that, as the irrelevant dimension, symbolic and nonsymbolic numerical magnitudes both automatically influenced processing, but symbolic numerical magnitudes influenced the processing of nonsymbolic numerical magnitudes more than nonsymbolic numerical magnitudes influenced the processing of symbolic numerical magnitudes. Moreover, numerical distance influenced the automatic processing of nonsymbolic numerical magnitudes more than it influenced the processing of symbolic numerical magnitudes. Together, these findings indicate that symbolic numerical magnitudes are processed more automatically that nonsymbolic numerical magnitudes.

The finding that symbolic and nonsymbolic numerical magnitude processing influence each other aligns with the dominant perspective in the field of numerical cognition that the same system is used to process symbolic and nonsymbolic numerical magnitudes (e.g., Cantlon et al., 2009; Dehaene, 2007; Dehaene et al., 1998; Nieder & Dehaene, 2009; Piazza et al., 2007). However, taken together, the results from chapter 4 provide strong evidence that the processing of symbolic and nonsymbolic numerical magnitudes is asymmetrical. Indeed, symbolic numerical magnitudes are processed more automatically than nonsymbolic numerical magnitudes. This finding could be taken to suggest that symbols may not simply be labels for pre-existing representations of nonsymbolic numerical magnitudes. Moreover, these data suggest that a representation of a nonsymbolic numerical magnitude does not need to be accessed to *automatically* process the semantic meaning of a symbolic numerical magnitude. In view of this, it should be considered that symbols may not be supported by a system that evolved to process nonsymbolic numerical magnitudes, but instead, by a superficially similar but ultimately distinct system (Lyons & Beilock, 2018; Núñez, 2017).

6.3 A Symbolic Number System

The predominant view in the field of numerical cognition is that symbolic numerical magnitudes are processed using the system that evolved to process nonsymbolic numerical magnitudes (e.g., Cantlon, 2012; Dehaene, 2007, 2008; Feigenson, 2007; Lyons & Ansari, 2009; Nieder & Dehaene, 2009; Piazza, Pinel, Le Bihan, & Dehaene, 2007). However, the findings presented in chapter's 2, 3 and 4 of the current thesis align with the growing body of data that indicate that symbolic numerical magnitudes are processed using a system that is distinct from the evolutionarily ancient system that is thought to support nonsymbolic numerical magnitude processing in the adult human brain (e.g., Krajcsi et al., 2016; Lyons et al., 2012, 2014). In view of this, it has been suggested that number symbols constitute a separate system in which the processing of symbols can be performed independently from accessing nonsymbolic representations of the quantities the symbols represent (Krajcsi, 2017; Krajcsi et al., 2018; Lyons et al., 2014; Lyons & Beilock, 2018; Núñez, 2017). This idea, that symbols constitute their own system and can be conceptualized without accessing representations of associated nonsymbolic numerical magnitudes motivations the question: what is the representational structure of the symbolic number system? In the following two paragraphs I speculate on the representational structure of the symbolic number system.

A key element of numerical symbols that differentiates them from the nonsymbolic numerical magnitudes that the symbols represent is that while nonsymbolic numerical magnitudes can only be represented approximately, symbols can and in fact must be represented exactly. Therefore, while nonsymbolic numerical magnitudes may be processed using an analogue number system (ANS), in which the representations are noisy or approximate (Cantlon, 2012; Dehaene, 2007; Dehaene et al., 1998; Moyer & Landauer, 1967) the processing of symbols is likely supported by a different more exact system. Broadly, it has been suggested that symbols are understood based on their associations with other symbols (For a comprehensive review see, Núñez, 2017). A discrete semantic system (DSS) has been proposed as a potential candidate for a system that represents symbolic numbers (Krajcsi et al., 2016). The DSS operates using a network that resembles a conceptual network or mental lexicon. In the DDS system, symbolic numerical magnitudes are stored within a network with each symbolic numerical magnitude acting as a node. The strength of the connections between the nodes (i.e., the symbolic numerical magnitudes) would be proportional to the strength of the semantic relations between the numbers, thus producing a distance effect. Recent behavioural data assessed whether symbolic and nonsymbolic numerical magnitude processing is more likely to be sub-served by a single system or two distinct systems (Krajcsi, 2017). Krajcsi and colleagues argued that if nonsymbolic and symbolic numerical magnitudes are supported by the same system, the distance and size effects should correlate with each other within formats, and the symbolic distance and size effects should correlate with the nonsymbolic distance and size effects. Results revealed that while distance and size effects correlate with each other for nonsymbolic numerical magnitude processing, the distance and size effects did not correlate with each other for symbolic numerical magnitude processing. Moreover, the nonsymbolic effects (distance and size) did not correlate with the symbolic effects (Krajcsi, 2017). In view of this, it is more likely that nonsymbolic and symbolic distance effects are sub-served by distinct systems. This data converges with other related research to support the finding that nonsymbolic numerical magnitudes are supported by an approximate number system, whereas symbolic numerical magnitudes are supported by the DSS (Krajcsi, 2017; Krajcsi et al., 2016, 2018; Lyons et al., 2015). This growing body of research supports the idea that a semantic network model may be a better candidate than the evolutionarily ancient approximate number system to explain the processing of symbolic numerical magnitudes in human adults.

At the neural level, the representational patterns of activation that underpin symbolic numerical magnitude processing is dissimilar to the representational patterns of activation that support nonsymbolic numerical magnitude processing (Bulthé et al., 2014; Damarla & Just, 2013; Lyons et al., 2014). Indeed, the representational structure of the neural activity that supports the processing of nonsymbolic numerical magnitude aligns with predictions of representational structures that would arise from nonsymbolic numerical magnitude processing being supported by an analogue approximate number system. Specifically, the representation patterns of activation associated with the nonsymbolic numerical magnitudes relate to each other as a function of ratio (Bulthé et al., 2014;

Damarla & Just, 2013; Lyons et al., 2014). In contrast, the patterns of neural representations supporting symbolic numerical magnitude processing do not vary systematically as a function of ratio (Bulthé et al., 2014; Damarla & Just, 2013; Lyons et al., 2014). Instead, the representational structure of symbolic numerical magnitude processing aligns with a semantic network model in which symbolic numerical magnitudes operate like discrete categories that relate to one another based on lexical frequency (Lyons & Beilock, 2018). Although this work is in its infancy, the combination of this behavioural and neuroimaging data provides compelling evidence that symbolic numerical magnitude processing is supported by a semantic representational system rather than the evolutionarily ancient approximate number system that supports nonsymbolic numerical magnitude processing in human adults. The findings from the current thesis, that symbols are processed more distinctly from nonsymbolic numerical magnitudes both at the neural and behavioural level in adult and children lends further support to this account.

6.4 The Emergence of Symbolic Thinking

The majority of research reviewed above indicating that symbolic and nonsymbolic numerical magnitudes are supported by two distinct systems has been conducted in human adults and older children, who have already learned the semantic meaning of symbolic numerals. However, in order to have a comprehensive understanding of the system that supports the processing of symbolic numerical magnitudes, it is necessary to explore how children acquire an understanding of the semantic meaning of these arbitrary symbols. Indeed, this question of how children acquire the semantic meaning of a symbol (such as a number word), often referred to as the "symbol-grounding problem," is a key problem within the field of numerical cognition (Leibovich & Ansari, 2016), and cognition more broadly (Coolidge & Overmann, 2012; Harnad, 1990).

Based on the dominant theory in the field of numerical cognition (Dehaene et al., 1998; Dehaene, 2007; Cantlon, 2012), that an evolutionarily ancient approximate number system supports the processing of both symbolic and nonsymbolic numerical magnitudes, it has been predicted that children learn the meaning of symbolic numerical magnitudes by mapping an arbitrary symbolic label onto the pre-existing representation supporting the corresponding nonsymbolic numerical magnitude (For review see: Leibovich and Ansari, 2016). However, the growing body of evidence, including from chapters 2-4 of this thesis, reveal that symbolic and nonsymbolic numerical magnitudes are likely supported by distinct systems suggests that the acquisition of symbolic number processing may not be a straightforward mapping of symbols onto pre-existing representations.

Indeed, based on the finding that symbolic and nonsymbolic numerical magnitudes are supported with distinct systems, it is conceivable that the acquisition of the semantic meaning of symbolic numerical magnitudes actually constrains the pre-existing representations that support nonsymbolic numerical magnitudes (Barner, 2017; Merkley & Ansari, 2016). More specifically, it can be hypothesized the process of learning the semantic meanings of number words influences how salient the property of quantity is to a child when interacting with a nonsymbolic numerical magnitude (Barner, 2017; Merkley & Ansari, 2016). In other words, learning the semantic meaning of number words may direct children's attention toward discrete quantities as a relevant dimension to attend to when examining and interacting with a set of objects that contains a variety of other non-numerical dimensions, such as non-numerical magnitudes, colours, and object types (Merkley, Scerif, & Ansari, 2017; Mix, Levine, & Newcombe, 2016). Taking a developmental approach to explore how acquiring knowledge of symbolic numerical magnitudes relates to the processing of nonsymbolic numerical magnitudes is a key avenue to enhance our understanding of how humans process symbolic and nonsymbolic numerical magnitudes across developmental time.

Consequently, in chapter 5 of the current thesis, I used a developmental approach to explore whether the acquisition of verbal number words relates to the degree to which children spontaneously attend to nonsymbolic numerical magnitudes in the world. Specifically, I developed and used a matching task called, "The Train Task," to measure whether children spontaneously used a number strategy or physical size strategy to build a train that "matched" a train built by an experimenter. During this task, an experimenter built a train using five or fewer blocks using sets of blocks where the length of the child's blocks differed from the length of the experimenter's blocks. The experimenter then said to the child “make your train the same as mine”. Results revealed that for small numbers (i.e., train’s that were made of two and three blocks) preschool-aged children used a number strategy on trials for which they knew the verbal number word that corresponded to the number of blocks that made up the train. However, children used a size strategy more than a number strategy on trials with five blocks, regardless of verbal number knowledge. These data indicate that verbal number word knowledge relates to the degree to which preschool-aged children attend to nonsymbolic numerical magnitudes, specifically for small numbers. Together, this suggests that when children learn the semantic meaning symbolic numerical magnitudes, it changes the way that they attend to small nonsymbolic numerical magnitudes in the world.

This finding from chapter 5, that children’s performance on a nonsymbolic numerical magnitude matching task is be limited by their knowledge of the meaning of number words provides support for developmental theories (Barner, 2017; Merkley & Ansari, 2016; Mussolin, Nys, Leybaert, et al., 2014) suggesting that learning the semantic meaning of symbols might affect the processing of nonsymbolic numerical magnitudes. Moreover, while this data cannot speak to whether children *can* conceptualize nonsymbolic numerical magnitudes prior to acquiring knowledge of symbolic numerical magnitudes, it certainly suggests that children who do not have knowledge of symbolic numerals do not spontaneously attend to nonsymbolic numerical magnitudes. In summary, the findings from this study relate to previous research in the field to support the idea that the evolutionarily ancient capacity to process nonsymbolic numerical magnitudes and the culturally acquired capacity to process symbolic numerical magnitudes are related across development (For review see: Mussolin et al., 2014). However, the findings from the current study also provide novel evidence for the less explored idea that learning the semantic meaning of symbolic numerical magnitudes, (i.e., forming a symbolic number system) may actually refine approximate representations of nonsymbolic numerical magnitudes.

6.5 Implications

Together, the four studies reported in this thesis provide novel insights into the relationship between symbolic and nonsymbolic numerical magnitudes in both children and adults. Several of the studies in this thesis identify how this relationship between symbolic and nonsymbolic numerical magnitudes can be influenced by an attentional state. The key finding from the data presented in the current thesis is that the way humans process symbolic numerical magnitudes is quite distinct from the way humans process nonsymbolic numerical magnitudes. Specifically, the behavioural and neural signatures associated with processing symbolic numerical magnitudes diverge from those that are associated with the processing of nonsymbolic magnitudes across methodologies, attentional conditions, and developmental periods. These findings, namely that the culturally acquired symbolic number system is more distinct from the evolutionarily ancient nonsymbolic numerical magnitude system than previously assumed has several important implications for how to support children's learning of early mathematical concepts.

The dominant assumption in the field, that symbols are learned by mapping arbitrary symbolic labels onto pre-existing representations of quantities has led researchers to attempt to improve symbolic numerical abilities by training students on nonsymbolic numerical magnitude processing (Hyde, Khanum, & Spelke, 2014; Kuhn & Holling, 2014; Obersteiner, Reiss, & Ufer, 2013; Park & Brannon, 2013; Sasanguie et al., 2013). Overall, there is no conclusive evidence that training nonsymbolic numerical magnitude processing improves symbolic mathematical competence (For review see: Szűcs & Myers, 2017). The findings reported in the current thesis supporting the idea that symbolic and nonsymbolic numerical magnitudes are processed using distinct systems help illuminate why these nonsymbolic numerical magnitude training programs do not lead to significant improvements in symbolic math. Indeed, training nonsymbolic numerical magnitude processing likely does not lead to improvements in symbolic math because the system that is being trained (i.e., the evolutionarily ancient nonsymbolic number processing system) is a similar but ultimately separate from the system that supports symbolic mathematical thinking (i.e., the symbolic number system). In view of this, it is not surprising that these training studies have resulted in null findings. Consequently, the findings from the current thesis can be taken to suggest that efforts to train early numerical concepts should be focussed on training the symbolic number system, rather than the system that evolved to process approximate nonsymbolic numerical magnitudes.

Relatedly, a focus of early mathematical learning has been on teaching children the link between symbolic and nonsymbolic numerical magnitudes, often referred to as mapping (Barth, Starr, & Sullivan, 2009; Huang, Spelke, & Snedeker, 2010; Le Corre & Carey, 2007; Lipton & Spelke, 2005, 2006; Odic, Le Corre, & Halberda, 2015). Recent research has implicated this ability to map symbols onto nonsymbolic numerical magnitudes as being important for later mathematical achievement (Libertus, Odic, Feigenson, & Halberda, 2016). Although mapping for small numbers is likely an important skill for children to master at a particular point during development, findings from the current thesis imply that the ability to map symbols onto their corresponding nonsymbolic numerical magnitudes is a necessary but not a sufficient condition for children to form a symbolic number processing system. In other words, in order for humans to develop a system that processes exact symbolic numerical magnitudes, children need to acquire knowledge of the structure of the symbolic number system, such as the learning that symbolic numerical magnitudes have an order and a lexical frequency, in addition to learning the semantic meaning of a symbolic numerical magnitude. Together, findings from the current thesis can be used to inform our understanding of what basic number processing abilities must be learned to facilitate a child's development of a comprehensive semantic system that can be used to support the higher-level processing of symbolic numerical magnitudes.

6.6 Limitations and Future Directions

The limitations associated with each specific study are reported in the discussion sections of each individual empirical chapter. However, in addition to the specific limitations discussed in the individual chapters, there are several broad limitations. In what follows, I will present and discuss these broad limitations and outline future directions that arise from these limitations, as well as provide future directions that go beyond simply addressing limitations.

As outlined in the introduction of this thesis, the processing of nonsymbolic numerical magnitudes is inherently confounded by non-numerical magnitudes such a physical size (For review see: Leibovich and Henik, 2013). It was not possible to control for non-numerical magnitudes in the meta-analysis, as this methodology requires using previously collected data. There was a large amount of variability in the degree to which the empirical studies included in the meta-analysis controlled for non-numerical magnitude processing. However, in the three other empirical chapters presented in the current thesis (chapters 3-5), I included controls for the effect of non-numerical magnitudes. In chapter 3 and 5, I included physical size as a variable of interest in order examine the neural representations supporting nonsymbolic numerical magnitudes (chapter 3) and degree of attention directed toward nonsymbolic numerical magnitudes (chapter 5), compared to physical size. In chapter 4, I included '*'s rather than blank spaces in the arrays with the goal of ensuring that arrays with more symbols did not take up more physical space. Critically, although I was cognizant of this need to account for the effect of non-numerical magnitudes on nonsymbolic numerical magnitude processing in some way, and included the optimal control variables whenever possible, there is no way to create stimuli where at least one non-numerical magnitude (e.g., size, density, convex hull) does not correlate with nonsymbolic numerical magnitude (Leibovich & Henik, 2013). Indeed, the natural correlation between nonsymbolic numerical magnitudes and non-numerical magnitudes makes it nearly impossible to study nonsymbolic numerical magnitude processing in isolation from non-numerical magnitudes. This tight link between the processing of nonsymbolic numerical magnitudes and non-numerical magnitudes is reflected in the findings from the parallel adaptation study reported chapter 3, showing that the brain region in the right intraparietal sulcus that is associated with nonsymbolic numerical magnitude processing is completely overlapping with the region associated with non-numerical magnitude processing. Therefore, a key limitation of the current thesis is that the results associated with nonsymbolic numerical magnitude processing may be influenced by correlated non-numerical magnitudes. This interesting inherent limitation with studying nonsymbolic numerical magnitude processing leads to an important future direction. Namely, future research should not rest upon the assumption that nonsymbolic numerical magnitudes are processed using a specific system that only processes discrete magnitudes. Instead, future research should explore the link between the processing of symbolic numerical magnitudes, compared to the processing of nonsymbolic numerical magnitudes as well as non-numerical magnitudes. Additionally, future research should test the role of non-numerical magnitude processing in the formation of the symbolic number system (Leibovich et al., 2017).

Another limitation associated with the experimental empirical studies included in this thesis is that, due to time constraints within the testing sessions, we were unable to include trial types that were of interest. Specifically, in the fMRI adaptation study (chapter 3), we were only able to include a single deviant type within each condition. For example, symbolic distance 1 only included the condition where the symbol six became the symbol seven. This is because within a habituation paradigm each deviant trial must be preceded by five to nine habituation trials. Including a small and large change of a symbolic, nonsymbolic and physical size condition required participants to remain still and attentive during a passive viewing task in an fMRI scanner for an hour. For this chapter, the decision was made to use fewer than optimal different trial types in order to increase the proportion of participants were able to remain still and attentive. Additionally, it was important to make this paradigm as concise as possible in order to have to option to implement this paradigm in a sample of children in the future. Critically, with the included number of trial types, only 45 of the 52 adult participants successfully passed the criteria for attention and motion. Relatedly, in chapter 4, all trials included in the study used the same two symbolic and nonsymbolic numerical magnitudes within each trial. For example, in a condition where the symbol was ‘2’ and ‘4’ the quantities were also two and four either congruently (i.e., two ‘2’s vs. four ‘4’s) or incongruently (i.e., two ‘4’s vs. four ‘2’s). It would have been ideal to include all combinations of symbolic and nonsymbolic numerical magnitudes (as has been done with the original Numerical Stroop task: Leibovich, Diesendruck, Rubinsten, & Henik, 2013). However, as this was the first study to implement a Symbolic-Nonsymbolic Stroop task, I included more trial types within conditions, rather than fewer trial types across many conditions. In view of this, I was unable to examine the effect of differentially varying the distance of the relevant dimension compared to the irrelevant dimension. In a future study, it would be ideal to compare participant's speed and accuracy for trials where the distance of the relevant condition is different from the distance in the irrelevant condition. Finally, in chapter 5, there were many additional conditions that I was interested in examining. For example, I could have included conditions where I changed the colours of the trains, manipulated the ratio between the experimenter's block size and the child's block size, built the trains behind a screen, included longer train lengths (beyond five cars), and/or adjust the language of the instructions. However, as the sample of participants in this study were between the ages of three and six years, the maximum duration that the participants were able to remain attentive was approximately 30 minutes. Therefore, I chose a single set of conditions that best supported my key research questions. Future studies should examine whether verbal number knowledge continues to relate to the degree to which young children spontaneously attend to nonsymbolic numerical magnitudes under different experimental conditions.

A final limitation that is specific to the neuroimaging studies is the fact that the vast majority of the participants in the meta-analysis (>98%), and all participants in chapter 3 of the current thesis are right-handed. Recent research indicated that association between the passive processing of symbolic numerical magnitudes and activation in the left parietal lobule was significant in a sample of right, but not left-handed individuals (Goffin, Sokolowski, Slipenski & Ansari, accepted 2019). Future research is needed to further examine similarities and differences in the neural correlates of symbolic compared to nonsymbolic numerical magnitude processing in left-handed compared to right-handed individuals.

There are several additional future directions that are unrelated to the limitations of the current chapters. Specifically, the possible co-existence of domain-specific neural processes underlying numerical magnitude processing adults (reported in chapters 2-4), raises questions about developmental trajectories of the systems underlying basic number processing. An important avenue for future research is to conduct follow-up studies where children complete the Symbolic-Nonsymbolic Stroop task and the Parallel Adaptation task, to study developmental specialization of the symbolic number system. More specifically, the paradigms developed for this thesis can be used cross-sectionally and/or longitudinally to examine age-related changes in the systems that support symbolic, nonsymbolic and non-numerical magnitudes.

Moving forward, a fundamental goal for the field of numerical cognition should be to understand individual differences in the way children learn symbolic numbers and to use this knowledge in pursuit of optimized learning processes across development. Once we as a field have reached a foundational understanding of the basic neuropsychological mechanisms supporting symbolic number learning, it will be of critical importance to focus on individual differences. A large body of future research is needed to unravel the key question of why learning math is easy for some children and so challenging for others.

6.7 General Conclusion

In conclusion, the body of research presented above has identified and described the behavioural and neural signatures of symbolic compared to nonsymbolic numerical magnitude processing. I identified converging brain activation associated with symbolic and nonsymbolic numerical magnitude processing across all previously conducted neuroimaging research (chapter 2) and examined the neural correlates of symbolic and nonsymbolic numerical magnitude processing in the absence of task demands (chapter 3). Additionally, I explored the role of attention on behavioural signatures of symbolic compared to nonsymbolic numerical magnitude processing in human adults (chapter 4). Finally, I investigated how learning symbolic numerical magnitudes relates to attending to nonsymbolic numerical magnitudes in young children (chapter 5).

Studying the neurobiology of numeral magnitude processing is necessary to elevate our understanding of how culturally-mediated information interacts with and potentially even shapes biologically endowed systems in the human brain. This enhanced understanding of the neuropsychological foundation that supports the uniquely human capacity for symbolic thinking could simultaneously inform and inspire critical developments to math education practices and policy and illuminate the multifaceted and dynamic interplay underlying the uniquely human capacity for complex learning.

6.8 References

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Appendices

Appendix A: Documentation of Ethics Approvals

Western Research

Research Ethics

Western University Health Science Research Ethics Board
HSREB Full Board Initial Approval Notice

Principal Investigator: Prof. Daniel Ansari
Department & Institution: Social Science\Psychology, Western University

Review Type: Delegated
HSREB File Number: 107423
Study Title: The neural basis of size and number
Sponsor: Natural Sciences and Engineering Research Council

HSREB Initial Approval Date: December 23, 2015
HSREB Expiry Date: December 21, 2016

Documents Approved and/or Received for Information:

Document Name	Comments	Version Date
Assent	App. P_Assent Letter	2015/11/05
Other	App. Q_summary of sub study procedure and sample size	2015/11/05
Recruitment Items	App. L_Telephone_Script_neural basis_children-Stage 3	2015/11/05
Recruitment Items	App. K_Recruitment_Email_stage 3	2015/11/05
Other	App. J_Recruitment procedure stage 2	2015/11/05
Recruitment Items	App. G_Recruitment poster fmri- Stage 2	2015/11/05
Other	App. H_fMRI safety questionnaire	2015/11/05
Other	App. I_Recruitment procedure for stage 1	2015/11/05
Other	App. F_wiat part 1	2015/11/05
Other	App. F_wiat part 2	2015/11/05
Other	App. F_wiat part 3	2015/11/05
Other	App. E_TEMA_1	2015/11/05
Other	App. E_TEMA_2	2015/11/05
Other	App. E_TEMA_3	2015/11/05
Other	App. D_wj quantitative concepts 1	2015/11/05
Other	App. D_wj quantitative concepts 2	2015/11/05
Other	App. D_wj quantitative concepts 3	2015/11/05
Recruitment Items	pp. B_SONA neural basis- Stage 1	2015/11/04
Other	App. C_ Examples of stimuli	2015/11/05
Recruitment Items	App. A_Recruitment poster- Stage 1	2015/11/05
Other	App. L - clean	2015/12/10
Letter of Information & Consent	Stage 1	2015/12/23
Letter of Information & Consent	Stage 2	2015/12/23

Western University, Research, Support Services Bldg., Rm. 5150
London, ON, Canada N6G 1G9 [redacted] www.uwo.ca/research/ethics

Western Research | **Research Ethics**

Letter of Information & Consent	Stage 3	2015/12/23

The Western University Health Science Research Ethics Board (HSREB) has reviewed and approved the above named study, as of the HSREB Initial Approval Date noted above.

HSREB approval for this study remains valid until the HSREB Expiry Date noted above, conditional to timely submission and acceptance of HSREB Continuing Ethics Review.

The Western University HSREB operates in compliance with the Tri-Council Policy Statement Ethical Conduct for Research Involving Humans (TCPS2), the International Conference on Harmonization of Technical Requirements for Registration of Pharmaceuticals for Human Use Guideline for Good Clinical Practice Practices (ICH E6 R1), the Ontario Personal Health Information Protection Act (PHIPA, 2004), Part 4 of the Natural Health Product Regulations, Health Canada Medical Device Regulations and Part C, Division 5, of the Food and Drug Regulations of Health Canada.

Members of the HSREB who are named as Investigators in research studies do not participate in discussions related to, nor vote on such studies when they are presented to the REB.

The HSREB is registered with the U.S. Department of Health & Human Services under the IRB registration number IRB 00000940.

[redacted]

Ethics Officer, on behalf of Dr. Joseph Gilbert, HSREB Chair

Ethics Officer to Contact for Further Information: Erika Basile ___ Nicole Kaniki ✓ Grace Kelly ___ Mina Mekhail ___ Vikki Tran ___

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Western Research

Research Ethics

Western University Health Science Research Ethics Board
HSREB Annual Continuing Ethics Approval Notice

Date: November 30, 2016
Principal Investigator: Prof. Daniel Ansari
Department & Institution: Social Science\Psychology,Western University

Review Type: Delegated
HSREB File Number: 107423
Study Title: The neural basis of size and number
Sponsor: Natural Sciences and Engineering Research Council

HSREB Renewal Due Date & HSREB Expiry Date:
Renewal Due -2017/11/30
Expiry Date -2017/12/21

The Western University Health Science Research Ethics Board (HSREB) has reviewed the Continuing Ethics Review (CER) Form and is re-issuing approval for the above noted study.

The Western University HSREB operates in compliance with the Tri-Council Policy Statement Ethical Conduct for Research Involving Humans (TCPS2), the International Conference on Harmonization of Technical Requirements for Registration of Pharmaceuticals for Human Use Guideline for Good Clinical Practice (ICH E6 R1), the Ontario Freedom of Information and Protection of Privacy Act (FIPPA, 1990), the Ontario Personal Health Information Protection Act (PHIPA, 2004), Part 4 of the Natural Health Product Regulations, Health Canada Medical Device Regulations and Part C, Division 5, of the Food and Drug Regulations of Health Canada.

Members of the HSREB who are named as Investigators in research studies do not participate in discussions related to, nor vote on such studies when they are presented to the REB.

The HSREB is registered with the U.S. Department of Health & Human Services under the IRB registration number IRB 00000940.

[redacted]

Ethics Officer, on behalf of Dr. Joseph Gilbert, HSREB Chair

Ethics Officer: Erika Basile ___ Katelyn Harris ___ Nicole Kaniki ✓ Grace Kelly ___ Vikki Tran ___ Karen Gopaul ___

Western Research

Research Ethics

Western University Non-Medical Research Ethics Board
NMREB Full Board Initial Approval Notice

Principal Investigator: Prof. Daniel Ansari
Department & Institution: Social Science\Psychology,Western University

NMREB File Number: 107807
Study Title: Developmental Trajectories of Basic Number Processing

NMREB Initial Approval Date: April 20, 2016
NMREB Expiry Date: April 20, 2017

Documents Approved and/or Received for Information:

Document Name	Comments	Version Date
Letter of Information & Consent	WJIII Reading Fluency	2016/02/24
Instruments	WJIII - Standardized test	2016/02/12
Instruments	WJIII - Standardized test	2016/02/12
Instruments	WJIII - Standardized test	2016/02/12
Instruments	WJIII - Standardized test	2016/02/12
Instruments	TEMA - Standardized test	2016/02/12
Instruments	TEMA - Standardized test	2016/02/12
Instruments	TEMA - Standardized test	2016/02/12
Instruments	WJIII - Standardized test	2016/02/12
Instruments	Examples of stimuli	2016/02/12
Data Collection Form/Case Report Form	Adult Demographics Questionnaire	2016/02/12
Western University Protocol	Received April 7, 2016	
Instruments	Parent Questionnaire - Received April 7, 2016	
Letter of Information & Consent	Parent Questionnaire LOI - Received April 7, 2016	
Letter of Information & Consent	Adult LOI Credit	2016/04/06
Letter of Information & Consent	Adult LOI Money	2016/04/06
Letter of Information & Consent	Child LOI	2016/04/06
Recruitment Items	Child Telephone Script	2016/04/06
Recruitment Items	Adult Recruitment Poster	2016/04/06
Recruitment Items	Adult SONA Script	2016/04/06
Recruitment Items	Child Recruitment Email	2016/04/06
Letter of Information	Information Letter to Preschools	2016/04/06
Instruments	HTKS Task A	2016/04/06
Instruments	HTKS Task B	2016/04/06

The Western University Non-Medical Research Ethics Board (NMREB) has reviewed and approved the above named study, as of the NMREB Initial Approval Date noted above.

NMREB approval for this study remains valid until the NMREB Expiry Date noted above, conditional to timely submission and acceptance of NMREB Continuing Ethics Review.

The Western University NMREB operates in compliance with the Tri-Council Policy Statement Ethical Conduct for Research Involving Humans (TCPS2), the Ontario Personal Health Information Protection Act (PHIPA, 2004), and the applicable laws and regulations of Ontario.

Members of the NMREB who are named as Investigators in research studies do not participate in discussions related to, nor vote on such studies when they are presented to the REB.

The NM[redacted]ment of Health & Human Services under the IRB registration number IRB 00000941.

[redacted]

Ethics Officer, on behalf of Dr. Riley Hinson, NMREB Chair

Ethics Officer to Contact for Further Information: Erika Basile ___ Nicole Kaniki ___ Grace Kelly ___ Katelyn Harris ___ Vikki Tran ___

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Western Research

Research Ethics

Western University Non-Medical Research Ethics Board
NMREB Amendment Approval Notice

Principal Investigator: Prof. Daniel Ansari
Department & Institution: Social Science\Psychology,Western University

NMREB File Number: 107807
Study Title: Developmental Trajectories of Basic Number Processing

NMREB Revision Approval Date: May 16, 2017
NMREB Expiry Date: April 20, 2018

Documents Approved and/or Received for Information:

Document Name	Comments	Version Date
Revised Western University Protocol	Received April 21, 2017.	

The Western University Non-Medical Science Research Ethics Board (NMREB) has reviewed and approved the amendment to the above named study, as of the NMREB Amendment Approval Date noted above.

NMREB approval for this study remains valid until the NMREB Expiry Date noted above, conditional to timely submission and acceptance of NMREB Continuing Ethics Review.

The Western University NMREB operates in compliance with the Tri-Council Policy Statement Ethical Conduct for Research Involving Humans (TCPS2), the Ontario Personal Health Information Protection Act (PHIPA, 2004), and the applicable laws and regulations of Ontario.

Members of the NMREB who are named as Investigators in research studies do not participate in discussions related to, nor vote on such studies when they are presented to the REB.

The NMREB is registered with the U.S. Department of Health & Human Services under the IRB registration number IRB 00000941.

[redacted]

Ethics Officer, on behalf of Dr. Riley Hinson, NMREB Chair
EO: Erika Basile ___ Grace Kelly ✓ Katelyn Harris___ Nicola Morphet ___ Karen Gopaul ___

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Western Research

Research Ethics

Western University Non-Medical Research Ethics Board

NMREB Annual Continuing Ethics Approval Notice

Date: April 17, 2017
Principal Investigator: Prof. Daniel Ansari
Department & Institution: Social Science\Psychology,Western University

NMREB File Number: 107807
Study Title: Developmental Trajectories of Basic Number Processing

NMREB Renewal Due Date & NMREB Expiry Date:
Renewal Due -2018/03/31
Expiry Date -2018/04/20

The Western University Non-Medical Research Ethics Board (NMREB) has reviewed the Continuing Ethics Review (CER) form and is re-issuing approval for the above noted study.

The Western University NMREB operates in compliance with the Tri-Council Policy Statement Ethical Conduct for Research Involving Humans (TCPS2), Part 4 of the Natural Health Product Regulations, the Ontario Freedom of Information and Protection of Privacy Act (FIPPA, 1990), the Ontario Personal Health Information Protection Act (PHIPA, 2004), and the applicable laws and regulations of Ontario.

Members of the NMREB who are named as Investigators in research studies do not participate in discussions related to, nor vote on such studies when they are presented to the REB.

The NMREB is registered with the U.S. Department of Health & Human Services under the IRB registration number IRB 00000941.

[redacted]

Ethics Officer, on behalf of Dr. Riley Hinson, NMREB Chair

EO: Erika Basile___Grace Kelly ___ Katelyn Harris___ Nicola Morphet ___ Karen Gopaul ___

Western University, Research, Support Services Bldg., Rm. 5150
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Curriculum Vitae

Name:	Helen Moriah Sokolowski
Post-secondary Education and Degrees:	The University of Western Ontario London, Ontario, Canada 2009-2013 B.A.
	The University of Western Ontario London, Ontario, Canada 2013-2015 M.A.
	The University of Western Ontario London, Ontario, Canada 2015-2019 Ph.D.
Honours and Awards:	Province of Ontario Graduate Scholarship ($15 000) 2018-2019
	Western Graduate Research Scholarship ($13 217) 2018-2019
	NSERC Alexander Graham Bell Canada Graduate Scholarship (CGS-D) ($105 000) Doctoral Scholarship 2015-2018
	Doctoral Excellence Research Award ($10 000) 2016-2017
	Western Graduate Research Scholarship ($5900) 2016-2017
	Marilyn (Pack) McClelland Award in Psychology ($750) Spring, 2016
	Western Graduate Research Scholarship ($8000) 2015-2016
	Western Graduate Research Scholarship ($10 000) 2015-2016
	NSERC Alexander Graham Bell Canada Graduate Scholarship (CGS-M) ($17,500) Masters Scholarship 2013-2014

Western Graduate Research Scholarship ($1500)
2013-2014

Clark and Mary J. Wright Scholarship ($1000)
Spring, 2013

Deans Honour List
2010-2013

Institute of Medical Sciences Best Poster Presentation Award ($50)
Summer, 2012

Summer Undergraduate Research Scholarship ($2400)
Summer, 2012

Summer Undergraduate Research Scholarship ($2400)
Summer, 2011

Summer Undergraduate Research Scholarship ($2400)
Summer, 2010

University of Western Ontario Entrance Scholarship ($2000)
2009-2010

David Oucherlony Leadership Award ($50)
2009

Related Work Experience

Teaching Assistant
The University of Western Ontario
3912G - Psychology of the Arts
Winter, 2019

Teaching Assistant
The University of Western Ontario
3480G – Research in Developmental Psychology
Winter, 2015

Teaching Assistant
The University of Western Ontario
2042A- Exceptional Children: Behaviour Disorders
Fall, 2014

Teaching Assistant

The University of Western Ontario
2043A- Exceptional Children: Developmental Disorders
Fall, 2014

Reporter for Child and brain development program meeting: Brain Development, cognition and education.
Canadian Institute for Advanced Research (CIFAR)
London, UK.
Summer, 2014

Teaching Assistant
The University of Western Ontario
3480G – Research in Developmental Psychology
Winter, 2014

Teaching Assistant
The University of Western Ontario
2042A- Exceptional Children: Behaviour Disorders
Fall, 2013

Teaching Assistant
The University of Western Ontario
2043A- Exceptional Children: Developmental Disorders
Fall, 2013

Research Assistant in the Numerical Cognition Laboratory
The University of Western Ontario
Winter, 2013

Research Assistant in Maternal Behavioural Neuroscience Laboratory
The University of Toronto, Mississauga
Summer, 2011, 2012, 2013

Research Assistant in the Cerebral Systems Laboratory,
The University of Western Ontario
2010-2011

Research Assistant in the Molecular Neuroscience of Schizophrenia Laboratory
The Centre for Addiction and Mental Health
University of Toronto
Summer, 2010
Research Assistant in the Insect Cold Tolerance Laboratory
The University of Western Ontario
2009-2010

Refereed Publications:

Colling, L., Holcombe, A. O., … Goffin, C., **Sokolowski, H. M.,** Ansari, D. … (Accepted, July 2019). Registered replication report of Fischer, Castel, Dodd, and Pratt (2003). *Psychological Science.* https://osf.io/he5za/

Goffin, C., **Sokolowski, H. M.,** Slipenkyj, M., Ansari, D. (Accepted, 2019). Does writing handedness affect neural representation of symbolic number? An fMRI Adaptation Study. *Cortex.*

Hawes, Z**., Sokolowski, H. M.,** Ansari, D. (In Press). Neural Underpinnings of Numerical and Spatial Cognition: An fMRI Meta-Analysis of Brain Regions Associated with Symbolic Number, Arithmetic, and Mental Rotation. *Neuroscience & Biobehavioral Reviews*.

Sokolowski, H. M., Hawes, Z., Lyons, I. M. (2019) What explains sex differences in math anxiety? A closer look at the role of spatial processing. *Cognition. 182*: 193-212, DOI: *10.1016/j.cognition.2018.10.005*

Sokolowski, H. M., Ansari, D. (2018) Understanding the effects of education through the lens of biology. *Nature Partner Journals Science of Learning. 3*(17): DOI: *10.1038/s41539-018-0032-y*

Anreiter, I., **Sokolowski, H.M.,** Sokolowski, M. B., (2017) Gene-environment interplay and individual differences in behaviour. *Mind, Brain, and Education.* 1-12, DOI:*10.1111/mbe.12158*

Sokolowski, H. M., Ansari, D. (2017) Math Anxiety: How it develops, what it does to the brain, and what to do about it. *Frontiers for Young Minds.* 5: 1-7. DOI*: 10.3389/frym.2017.00057.*

Sokolowski, H. M., Fias, C., Ononye, A, & Ansari, D. (2017) Are numbers grounded in a general magnitude processing system? A functional neuroimaging meta-

analysis. *Neuropsychologia. 105*, 50-69, DOI*: 10.1016/j.neuropsychologia.2017.01.019*

Sokolowski, H. M., Fias, W., Mousa, A, & Ansari, D. (2017) Common and distinct brain regions support symbolic and nonsymbolic numerical magnitude processing in humans: A functional neuroimaging meta-analysis. *Neuroimage. 1*(146): 376-394. DOI*: 10.1016/j.neuroimage.2016.10.028*

Sokolowski H. M., Vasquez, O. E., Unternaehrer, E., Sokolowski, D. J., Biergans, S. D., Atkinson, L., Gonzalez, A., Silveira, P. P., Levitan, R., O'Donnell, K. J., Steiner, M. Kennedy, J. Meany, M. J., Fleming, A. S., Sokolowski, M. B. on behalf of the MAVAN and Toronto Longitudinal Cohort research teams. (2017) The Drosophila foraging gene human orthologue PRKG1 predicts individual differences in the effects of early adversity on maternal sensitivity. *Cognitive Development. 42*: 62-73, DOI*:10.1016/j.cogdev.2016.11.001*.

Sokolowski, H.M. & Ansari, D. (2016) Symbolic and nonsymbolic representation of number in the human parietal cortex: a review of the state-of-the art, outstanding questions and future directions. *Continuous Issues in Numerical Cognition*, San Diego, CA: Elsevier, 37-58. DOI: 10.1016/B978-0-12-801637-4.00015-9

Sokolowski, H. M., & Necka, E. A. (2016) Remediating math anxiety through cognitive training: Potential roles for math ability and social context. Journal of Neuroscience. Journal Club Article. *36*(5): 1439-1441. DOI: https://doi.org/10.1523/JNEUROSCI.4039-15.2016

Necka, E. A., **Sokolowski, H. M.**, Lyons, I.M. (2015) The role of self-math overlap in understanding math anxiety and the relation between math anxiety and performance. Journal of Neuroscience. Frontiers in Psychology - Cognition. *6*: 1542. DOI: 10.3389/fpsyg.2015.01543

Sokolowski, H. M., Clouston, B. J., Gill, G., Kim, C. & Worgan, R. (2013) Grass type, vegetation cover, and predation affect abundance of *Microtus californicus* and

Thomomys bottae in costal Mediterranean ecosystem. Immediate Science Ecology. *2*: 11-7. DOI: 10.7332/ise2013.2.2.dsc.

Menon, M., Quilty, L. C., Zawadzki, J. A., Woodward, T. S., **Sokolowski, H. M.,** Boon, H. S. & Wong, A. H. (2013). The role of cognitive biases and personality variables in subclinical delusional ideation. *Cognitive Neuropsychiatry. 18*(3):208-218. DOI: 10.1080/13546805.2012.692873.

Zawadzki, J. A., Woodward, T. S., **Sokolowski, H. M.,** Boon, H. S., Wong, A. H., & Menon, M. (2012). Cognitive factors associated with subclinical delusional ideation in the general population. Psychiatry Research. *Psychiatry Research. 197*(3):345-349. DOI: 10.1016/j.psychres.2012.01.004.

Nonrefereed Publication:

Sokolowski, H. M. (2014) Child and brain development program meeting: Brain development, cognition and education. Report for the 30th program meeting for the Canadian Institute for Advanced Research. London, UK.

International Oral Presentations:

Sokolowski, H. M., (2018, April) Learning verbal number words relates to how children attend to numerical quantity. Invited Speaker *Mathematical Cognition and Learning Society,* Oxford, UK.

Lyons, I., Daker, R. J., **Sokolowski, H. M.,** Hawes, Z., Ramierez, G., Maloney, E. A., Rendinia, D. N., Levine, S. C., Beilock, S. L. (2018, April) Spatial anxiety scale – A novel tool with applications for STEM education. *Mathematical Cognition and Learning Society,* Oxford, UK.

Sokolowski. H. M. & Ansari, D. (2016, April) Developmental changes in the neural correlates of symbolic number processing: A functional neuroimaging meta-analysis. Invited Speaker at the *"Typical and atypical development of numerical* *cognition: evidence from brain and behaviour"*, Jerusalem, Israel.

Sokolowski, H. M., Sokolowski, M. B. & Fleming, A. (2013, December) Gene-Environment Interplay: A MAVAN Study, *University of Toronto*.

International Poster Presentations:

Sokolowski, H. M., Hawes, Z., Peters, L., Ansari, D., (2019, June) Neural correlates of symbolic, nonsymbolic and non-numerical magnitude processing: An fMRI adaptation Study. *Mathematical Cognition and Learning Society,* Ottawa, ON, Canada.

Goffin, C., **Sokolowski, H. M.,** Slipenkyj, M., Ansari, D., (2019, June) Does writing handedness affect neural representation of symbolic number? An fMRI Adaptation Study. *Mathematical Cognition and Learning Society,* Ottawa, ON, Canada

Hawes, Z., **Sokolowski, H. M.,** Ononye, C., Ansari, D., (2019, June) Neural Underpinnings of Numerical and Spatial Cognition: An fMRI Meta-Analysis of Brain Regions Associated with Symbolic Number, Arithmetic, and Mental Rotation. *Mathematical Cognition and Learning Society,* Ottawa, ON, Canada

Sokolowski, H. M., Merkley, R., Bray Kingissepp, S. S., Vaikuntharajan, P., Ansari, D. A. (2018, September) Learning verbal number words relates to how children attend to numerical quantity. *International Mind, Brain and Education Society (IMBES),* Los Angeles, USA.

Sokolowski, H. M.*, Goffin, C.*, Matejko, A. A., Bugden, S., Lyons, I. M., Ansari, D. (2018, September) Assessing knowledge translation in the field of mind, brain, and education in pre-service teachers. *International Mind, Brain and Education Society (IMBES),* Los Angeles, USA.

*These authors contributed equally to the work

Gattas, S., Daker, R. J., **Sokolowski, H. M.,** Lyons, I. M., (2018, September) Predicting STEM-related academic outcomes with math anxiety and attitudes in university students. *International Mind, Brain and Education Society (IMBES),* Los Angeles, USA.

Daker, R. J., Gattas, S., **Sokolowski, H. M.,** Lyons, I. M., (2018, April) Effects of math anxiety and math ability on university mathematics engagement. *Mathematical Cognition and Learning Society,* Oxford, UK

Sokolowski, H. M., Hawes, Z, Leibovich, T. Ansari, D. A. (2017, May) The interference of symbolic and nonsymbolic numbers in a novel enumeration Stroop task. *Association for Psychological* Science, Boston, USA.

Sokolowski. H. M. & Ansari, D. (2016, June) Developmental changes in the neural correlates of number processing: A functional neuroimaging meta-analysis. *The European Association for Research on Learning and Instruction (EARLI) Special Interest Group 22 "Neuroscience and Education",* Amsterdam, Netherlands.

Sokolowski. H. M., Fias, W., & Ansari, D. (2015, October) Common and distinct brain regions support symbolic and nonsymbolic numerical magnitude processing: A functional neuroimaging meta-analysis. *Education and Neuroscience Symposium*, Hannover, Germany.

Sokolowski. H. M., Fias, W., & Ansari, D. (2015, September) Common and distinct brain regions support symbolic and nonsymbolic numerical magnitude processing: A functional neuroimaging meta-analysis. *Inaugural Brain and Mind Institute Symposium*, University of Western Ontario, London, ON.

Sokolowski. H. M., Fias, W., & Ansari, D. (2015, May) Are numbers specialized or grounded in a generalized for magnitude representation: A functional neuroimaging meta-analysis. *NIH Math Conference*, St. Louis, Missouri, USA.

Sokolowski. H. M., Fias, W., & Ansari, D. (2014, January) Are numbers specialized or grounded in a general magnitude system? A quantitative meta-analysis. *Lake*

Ontario Visionary Establishment (LOVE), Niagara Falls, Ontario Canada.

Matejko, A., **Sokolowski, H. M.,** & Ansari, D. (2013, April). Early numeracy skills in preschool and kindergarten children: an iPad pilot study. *Biennial Meeting of the Society for Research in Child Development*, Seattle, WA, USA.

Sokolowski, H. M., Matejko, A., & Ansari, D. (2013, April) Training of early numeracy skills in preschool and kindergarten: An iPad training study. *University of Western Ontario Honours Thesis Poster Day*, London Ontario.

Matejko, A., Erdeg, B., Lefcoe, A., **Sokolowski, H. M.,** & Ansari, D. (2012, September). Training early numeracy skills in Kindergarten children: and iPad pilot study. *Connaught Global Challenge Symposium, Institute for Human Development*, Toronto, Ontario. ***Award Winning Poster**

Browne, D.T., Agrati, D., Akbari, E., de Medeiros, C., **Sokolowski, H.M.,** Sokolowski, M.B., Kennedy, J., Meaney, M., Steiner, M & Fleming, A.S. (2012, September) Maternal anxiety from pregnancy to two years post-partum: Examining the interactive roles of 5-HTTLPR and early child trauma. *Connaught Global Challenge International Symposium, Institute for Human Development,* Toronto Ontario.

Sokolowski, H.M., Mileva-Seitz V., Kennedy, J.L., Meaney, M. J. Sokolowski, M. B., & Fleming, A. S. (2012, August) Corticotrophin Releasing Hormone Receptor 1 (CRHR1), life events and maternal behavior: A MAVAN Project. *University of Toronto Institute of Medical Sciences Research Day, Toronto Ontario*. ***Award Winning Poster**

Wonch, K.E., Steiner, M, de Medeiros, C.B., Barrett, J.A., **Sokolowski, HM.,** Fleming, A.S. & Hall, G. (2012, October) The neural correlates of responsiveness to infant cues in mothers with and without postpartum depression. *McMaster Brain and Body Conference*, Hamilton, Ontario.

Zawadzki, J.A., Menon, M., Quilty, L.C., Woodward, T.S., **Sokolowski, H.M.,** Boon, H.S. & Wong, A.H.C. (2012, July) Predictors of Sub-clinical delusional ideation in the general population. Centre for Addiction and Mental Health. *Gordon Conference on the neurobiology of cognition*, Lucca (Barga), Italy.

Sokolowski, H.M., Wonch, K., De Medeiros, D., Barrett, J., Hall, G., Steiner, M. & Fleming, A.S. (2011, August) fMRI activation patterns in new mothers suffering from post-partum depression in response to infant pictures. *University of Toronto Institute of Medical Sciences*, Toronto Ontario.

Sokolowski, H.M., John Zawadzki, Heather Boon, Mahesh Menon and Albert H. C. Wong (2010, August) Cognitive factors associated with belief formation in the general population. *University of Toronto Institute of Medical Sciences*, Toronto Ontario.

Media Contributions:

“A Brief Conversation” Radio Interview with Stephen Hurley at voicEd Radio, June 2019

“Learning Number Words in Preschool” Article in the Language, Reading & Math in Children Newsletter, University of Western Ontario, Volume 11, January 2018

Supervisory Experience:

Co-supervising Aymee Alvarez’s Master of Science Degree

Thesis Title: The neural representation of mirror numbers: An fMRI adaptation study. (September 2018-Present)

Co-supervised Sarah Samantha Bray Kingissepp’s Fourth Year Honours Thesis

Thesis Title: Does cardinal principle knowership predict the amount of number strategy used? (2017, April)

Lecturing Experience:

Sokolowski, H. M. (2018, February) From Gene to Brain. Guest Lecture in Course 3440B Developmental Cognitive Neuroscience, University of Western Ontario, London Ontario.

Sokolowski, H. M. (2015, Winter) Independently conducted a weekly tutorial on research methods in developmental psychology.

Tutorial topics: 1) Introduction to Research in Developmental Psychology, 2) Observational Research, 3) Collecting Data, 4) Interrater Reliability, 5) Data Entry and Analyses in SPSS

Sokolowski, H. M. (2014, October) Language Development. Guest Lecture in Course 2043A Exceptional Child: Developmental Disorders, University of Western Ontario, London Ontario.

Sokolowski, H. M. (2014, Winter) Independently conducted a weekly tutorial on research methods in developmental psychology.

Tutorial topics: 1) Introduction to Research in Developmental Psychology, 2) Observational Research, 3) Collecting Data, 4) Interrater Reliability, 5) Data Entry and Analyses in SPSS

Sokolowski, H. M. (2013, October) The development of early numeracy. Guest Lecture in Course 2043A Exceptional Child: Developmental Disorders, University of Western Ontario, London Ontario.

Community Outreach Oral Presentations:

Sokolowski, H. M. (2015, October) Symbolic and nonsymbolic numbers in the brain: A neuroimaging meta-analysis. High School Outreach Talk, London, ON.

Sokolowski, H.M., & Matejko, A. (2012, November) Early development of numeracy skills through technology. Presentation for teachers at London District School Board Professional Development Day.

Academic Activities:

Co-reviewer of the submitted cognitive posters for the Association for Psychological Science, May 2018, San Francisco, USA.

Co-reviewer of the submitted cognitive posters for the Association for Psychological Science, May 2017, Boston, USA.

Assistant to Conference Organizer of the International Mind, Brain and Education Conference, September 2016, Toronto Ontario.

Co-Organizer of the Developmental Brown Bag Series 2015/16 in the Department of Developmental Psychology at The University of Western Ontario, Canada.

Ad Hoc Reviews:

Frontiers Psychology

Frontiers for Young Minds (Science Mentor)

British Journal of Educational Psychology

Developmental Cognitive Neuroscience

Language Learning and Development

Psychonomic Bulletin & Review

Brain Structure and Function

Cognitive, Affective, & Behavioural Neuroscience

Advanced Courses/Workshops:

Statistical Horizons, Structural Equation Modelling. (July 11-15, 2016). Chicago, Illinois.

FMRIB Software Library (FSL) Course, Oxford University. (June 19-23, 2017). Vancouver, Canada.