#### A Sense of Order: Ordinality and the meaning of symbolic numbers

Ian M. Lyons

University of Chicago

# INTRODUCTION

How are symbolic numbers represented in the brain? The central conclusion of my thesis is that ordinality – the relative position of numbers – is central to answering this question. Furthermore, I show that efficient representation of ordinal information in symbolic numbers (e.g., Indo-Arabic numerals) is a crucial link between basic number representation and more complex mathematics. My thesis thus advances our understanding of the neurocognitive basis of symbolic number representation – a recent (circa 4000 BCE) human cultural invention that forms the foundation of our modern scientific world. My work also provides clear hypotheses about the key processes leading to the emergence of symbolic numbers in the developing brain, which in turn may directly inform early math-education practices.

Many species are capable of representing numbers nonsymbolically (e.g., roughly how many members are in our group versus theirs; Dehaene et al., 2003; Nieder, 2005; Agrillo et al., 2011). Humans are not exceptional in this respect, and this nonsymbolic system (commonly referred to as the approximate number system, or ANS) emerges very early in development (Ansari, 2008; Cordes & Brannon, 2008; Hyde & Spelke, 2010). Many have suggested that the meaning of symbolic numbers (e.g., Indo-Arabic numerals) is derived from the ANS (e.g., Nieder & Dehaene, 2009; Verguts & Fias, 2004). In Chapter 1 (also Lyons et al., 2012), I provide the first direct test for the translation between symbolic and nonsymbolic numbers in adults. The results show that the meaning of symbolic numbers is tied far less strongly to one's approximate number system than has been previously assumed (e.g., Nieder & Dehaene, 2009; Verguts & Fias, 2004).

What explains these divergent results (from prior work)? Further, if symbolic numbers do not draw their meaning from the ANS, then whence? In Chapter 2, I demonstrate that previous conclusions about the overlap between symbolic and nonsymbolic numbers have been drawn from work that has almost exclusively focused on one property of numbers: Cardinality. Cardinality answers the question, *How many*? It is the last number one says when counting a set of items. Consistent with prior work, I show that cardinal processing results in similar behavioral and neural patterns for both symbolic and nonsymbolic numbers.

A far less studied aspect of number representation is ordinality. *Ordinality* answers the question, *What position?* The ordinality of a given number tells you which number came previously, and which number comes next. In Chapter 2, using a combination of behavioral and multiple forms of neural evidence, I show that relative order is processed in fundamentally different ways for symbolic and nonsymbolic (ANS) numbers. In symbolic numbers, order is assessed via specialized retrieval processes which differ both behaviorally and neurally even from those seen for symbolic cardinal processing. In contrast, ordinality in nonsymbolic numbers is processed via iterative cardinal assessment. Ordinality is thus a key property that distinguishes symbolic from nonsymbolic number representation. Focusing on ordinality should thus lead to novel insights about the transition from approximate, nonsymbolic representation of number to the precision and efficiency of symbolic numbers that allows for more complex mathematics. Chapter 3 takes a major step in that direction.

In Chapter 3 (also Lyons & Beilock, 2011), I assess the functional relevance of ordinality in symbolic numbers for more complex mathematical processing. I show that one's ability to assess ordinal relations in symbolic numbers predicts one's complex mental-arithmetic ability: better ordinal assessment predicted better mental arithmetic. This relation obtained even when controlling for ordinal assessment in a non-numerical domain (letters), general cognitive (working memory) capacity, and nonsymbolic number processing. Furthermore, one's numerical symbol-ordering ability fully mediated (explained) the previously observed relation between ANS ability and more complex math abilities (e.g., Halberda et al., 2008). The ability to efficiently represent and access the order of numerical symbols thus appears to be a crucial stepping stone between the ANS and higher math abilities. Several developmental researchers (including myself) are now pursuing the developmental and educational implications of this claim. In this way, my work has the potential to directly inform early math-education practices.

My thesis draws upon multiple methodologies. Chapter 1 and part of Chapter 2 rely upon the power of traditional, mean-based behavioral measures to draw inferences about the nature of the representations that drive the observed behavior. In Chapter 2, I also draw upon the additional perspective neuroimaging (in this case fMRI) can give us. First, using mean-based neural analyses, I provide converging evidence for the notion that the similarities and differences between symbolic and nonsymbolic numbers follow the type of numerical processing in question: ordinal versus cardinal. Next, I again combine behavioral and neuroimaging techniques to reveal how ordinality is assessed in symbolic and nonsymbolic contexts. I also use a recently developed fMRI analysis technique, representational similarity analysis (Kriegeskorte et al., 2008) to provide further converging evidence for how the nature of symbolic number representation is fundamentally different from nonsymbolic

number representation. In Chapter 3, I rely on an individual differences approach to test the implications of the previous chapters in a more applied domain – mental arithmetic. Throughout my dissertation, I draw on literature and methods from a wide range of disciplines, including animal neuroscience, cognitive neuroscience in humans, computational modeling, and multiple behavioral domains including developmental research and work with adults.

This highly interdisciplinary view of how to approach the science of human behavior drove my graduate career as well. In addition to work done for my dissertation, I relied on methodologies from multiple domains to conduct research in a diverse range of research areas. These included behavioral and fMRI work on the experience-dependent nature of language processing (Beilock et al., 2008; Lyons et al., 2010), behavioral and fMRI work on the interplay between emotion and cognition in mathematics anxiety (Lyons & Beilock, 2012a, 2012b), and developmental work on how young children learn to use their environment for spatial navigation (Lyons et al., *in press*).

#### **Chapter 1 Summary**

In *Chapter 1* (Lyons et al., 2012), we directly test the proposition that the meaning of symbolic numbers is estranged from number representation in the ANS by asking participants to use numerical symbols in a context that forces them to access a sense of how much a given symbol represents directly. We asked participants to compare quantities represented either in symbolic (Arabic numeral or written numberword; Figure 1.1a,d) or nonsymbolic format (an array of dots flashed too briefly to count; Figure 1.1b,e). Crucially, we also had participants compare one quantity presented as a symbol to another quantity presented nonsymbolically (as an array of dots; Figure 1.1c,f).

If numerical symbols retain a strong link to an approximate sense of the quantities they represent, then mixing formats should be akin to comparing two entities that ostensibly differ only in representational quality (sharpness of approximate tuning-curves; Piazza et al., 2004; Merten and Nieder, 2009). Adults are faster and more accurate when comparing two numeral-stimuli than two dot-stimuli (Buckley and Gillman, 1974; Lyons and Beilock, 2009). Thus, replacing one dot-stimulus with a (superior) numeral-stimulus should improve mixed-format comparison performance (relative to dot-dot comparison). According to the hypothesis that symbolic and nonsymbolic quantity representations draw from the same neural populations (Dehaene, 2008; Santens et al., 2010), mixed-format comparisons (which combine a broadly tuned dot-stimulus with a finely tuned numeral-stimulus) in Experiments 1-2 should yield performance somewhere in between that of numeral-numeral (two finely tuned stimuli) and dot-

dot comparisons (two broadly tuned stimuli); or more conservatively, mixed performance should at least be no worse than dot-dot comparisons.

By contrast, if symbolic numbers have become detached from an intuitive sense of the nonsymbolic quantities to which they presumably refer, accessing this sense of quantity directly from a numerical symbol may incur an additional processing cost. Hence, mixed-format comparisons should lead to worse performance than either numeral-numeral or dot-dot comparisons.



Figure 1.1

Figure 1.1 shows examples of comparison tasks from Experiment 1 [a-c] and Experiment 2 [d-f]. ISI: inter-stimulus interval; ITI: inter-trial interval. NN: numeral-numeral; DD: dot-dot; MX: mixed-format. Trial-timing was the same for Experiments 2-3.

In Experiment 1, response-times were significantly longer for mixed-format than dot-dot trials in all categories [all  $ts(20) \ge 7.97$ , ps < .001,  $ds \ge 1.74$ ; Figure 1.2-top]. However, it may have been that the difference between dot-dot and mixed-format performance in Experiment 1 arose, not because of a weak link between the ANS and numerical symbols, but due to the cost of switching between different perceptual input streams. It may simply be that the cost of mixing formats in Experiment 1 was driven by the inability to switch between these perceptual input streams – and hence may say nothing about numerical representation per se.

To ensure this was not the case, in Experiments 2-3, we chose an inter-stimulus-interval (Figure 1.1d-f) that far exceeded (roughly doubled) the potential switch-cost window seen in Experiment 1 (maximum

switch-cost was 426msec, Figure 1.2-top). In Experiment 2, response-times remained significantly longer for mixed-format than dot-dot trials in all categories [all  $ts(20) \ge 3.07$ , ps < .001,  $ds \ge .67$ ; Figure 1.2-middle].





Figure 1.2 shows the cost (mean difference, in milliseconds) of mixing formats. Abbreviations: MX: mixedformat (symbolic/nonsymbolic in Experiments 1-2; symbolic/symbolic in Experiment 3); DD: dot-dot; NN: numeral-numeral. Red error-bars are 95% confidence intervals (all contrasts were within-subjects, two-tailed). Hence, if the lower bar crosses 0, there was no significant cost of mixing formats. Comparisons were subdivided into four categories: small-far, small-close, large-far, large-close. In all conditions, half of the trials were numerically small (1-4), and half were large (10,20,30,40); orthogonally, half of critical-trials were numerically close ( $|n_1-n_2| = 1,10$ ) and half were far ( $|n_1-n_2| = 2,3,20,30$ ).

In Experiment 3, we tested whether the potential cost of mixing formats observed in Experiments 1-2 might simply be due to mixing representational or visual format, rather than to asymmetric accessing of quantity information. We expected quantities presented as number-words to be represented symbolically, as in the case of numerals. We thus predicted that directly comparing a numeral with a number-word should not yield performance worse than word-word comparisons (which were expected to yield less efficient performance than numeral-numeral comparisons; Damian, 2004). This result would suggest that the performance degradation seen for mixed comparisons is not simply due to mixing representational or visual formats. Performance did not significantly differ between mixed-format and word-word conditions for either response-times ( $ps \ge .390$ ; Figure 1.2-bottom) or error-rates ( $ps \ge .636$ ).

In sum, Experiments 1 and 2 provide clear evidence that numerical comparisons between symbolic and nonsymbolic quantities are considerably more difficult than comparing two nonsymbolic quantities. One might expect the comparison of a highly accurate stimulus (numeral) and an inaccurate stimulus (dotarray) to be easier (or at least no worse) than comparison of two inaccurate stimuli (two dot-arrays). Our data reject this view and suggest instead that a numeral does not provide direct access to an approximate sense of the quantity it represents. Rather, it appears that additional, inefficient processing is required to compare symbolic with nonsymbolic quantities. Experiment 3 results are consistent with the hypothesis that switching between visual numerical formats – so long as both formats point to symbolic representations – does not incur the same cost that arises when switching between symbolic and nonsymbolic numerical formats. The data reported here plainly call into question the strength of the link between numerical symbols and a sense of the quantities they are meant to represent.

## **Chapter 2 Summary**

The results from Chapter 1 leave us with a simple question: if a symbolic number's meaning is not directly derived from the ANS, then whence? Working with ideas developed in Deacon (1997), Nieder (2009) proposed that symbolic numbers are first and foremost members of an associative system. In other words, the meaning of a number in this system is primarily derived from its relation to other symbols in the system (Wiese, 2003). These symbol-symbol associations may even come to overshadow the relation between a given number and its original ANS referent (a proposal consistent with the results in Chapter 1). Crutch & Warrington (2010) found that, somewhat consistent with an embodied cognition point of view, the meaning of concrete nouns (book, door, cat, computer) is strongly tied to perceptual representations of the noun's referent. By contrast, more abstract nouns (freedom,

happiness, probability, justice) derive their meaning more from their relation to other abstract nouns. In this view, one may imagine that symbolic numbers operate in a more abstract manner, and thus their meaning is more directly bound to how they relate to other numbers (Delazer & Butterworth, 1997).

## Figure 2.1



Figure 2.1 shows examples of each task in Chapter 2. Our experimental conditions of interest for the fMRI results may be divided along two orthogonal axes. One axis is symbolic versus nonsymbolic number representation. As in Chapter 1, symbolic refers to Indo-Arabic numerals, and nonsymbolic refers to arrays of dots presented too quickly to count. The second axis is cardinal versus ordinal. Cardinal judgments were made by assessing which of two numbers represented the greater quantity. Ordinal judgments were made by assessing whether three numbers were in order. (all three items were either in increasing or decreasing left-right order. Combining these two axes yields the four experimental conditions shown in Figure 2.1: numeral-comparison, numeral-ordering, dot-comparison, and dot-ordering. Control tasks involved luminance judgments that otherwise paralleled stimulus details and task demands of the experimental tasks.

What kind or kinds of associations may serve to link symbolic numbers to one another? One strong candidate is relative order, or ordinality. *Cardinality* answers the question, *How many*? It is the last number one says when counting a set of items, and it is by far the most studied aspect of number processing, whether at the behavioral or the neural level (see Dehaene, 2008). By contrast, *ordinality* answers the question, *What position*? The ordinality of a given number tells you which number came previously, and which number comes next. In essence, ordinality tells you how a number relates to its closest neighbors (although the principle can be extended to more distant numbers). The precision of the symbol 100 arises from the fact that we know it comes one after 99 and one before 101.

Consistent with this notion, for ordering trials with properly ordered numbers, distance-effects for symbolic numbers were reversed, such that performance was better on trials with distances of 1 (e.g.,

{5 6 7}) than on trials with distances of 2 (e.g., {4 6 8}; p=.018) (see Figure 2.2 in the main thesis document: Ord-Ord; white bars). Crucially, distance-effects for nonsymbolic numbers in this condition were not reversed, such that performance was better on trials with distances of 2 than on trials with distances of 1; p<.001). It thus appears that ordinality operates for symbolic numbers in a fundamentally different way than for nonsymbolic numbers. Conversely, the distance-effects for nonsymbolic numbers in the Ord-Ord condition was similar in magnitude to that seen for cardinality assessments (see grey bars labeled Comparison in Figure 2.2 in the main thesis document; p=.272). One possibility, then, is that assessing ordinality in nonsymbolic numbers operates in a manner similar to assessing cardinality. By contrast, ordinality and cardinality assessment may be qualitatively different for symbolic numbers. In support of this idea, unlike nonsymbolic numbers, distance-effects in the numeral ordering condition were significantly different than those seen in the numeral comparison condition (p=.007). We next turn to the fMRI data to test this hypothesis at the neural level.

We first sought to identify regions common to ordinal and cardinal processing in symbolic numbers, or, as would be consistent with the (reverse) distance-effect results discussed above, whether ordinality and cardinality operate differently for numerals. This was done using the conjunction of the two contrasts: NumOrd>Control, NumComp>Control. There were no significant regions at the threshold used for our other whole-brain contrasts (p<.005, $\alpha$ <.01). This was true even when we lowered the threshold to p<.10, uncorrected (1.1% of voxels showed overlap which was not different from the 1% predicted by chance). This is consistent with our hypothesis that ordinality and cardinality operate differently for numerals (and hence should show no neural overlap). Taken together with the reverse distance-effect seen only in symbolic ordinality and not symbolic cardinality judgments, we conclude that ordinality and cardinality are qualitatively different processes in symbolic numbers.

We next sought to identify regions that were common to both ordinal and cardinal processing in nonsymbolic numbers. Results revealed a primarily right-lateralized set of regions, including the anterior portion of the right IPS (IPSa; blue regions in Figure 2.2 of this document). These results are consistent with the notion that both ordinality and cardinality of nonsymbolic numbers involves activation of an area routinely seen for nonsymbolic number processing (Dehaene et al., 2003; Nieder & Dehane, 2009), regardless of the type of processing involved (ordinal versus cardinal). If ordinality is assessed in dots by iteratively comparing constituent pairs of dot arrays (iterative cardinality judgments), then one should call upon the same neural structure but simply to a greater extent: one would expect to see greater activity for the DotOrd relative to the DotComp task in neural regions similar to those found in the conjunction analysis performed above. Regions showing this effect are shown in red in Figure 2.2, and

voxels common to both analyses are shown in purple. Consistent with the iterative reuse hypothesis, right IPSa showed voxels common to both analyses (purple). Taken together with the behavioral distance-effect analysis above, these neural results are consistent with the notion that one assesses ordinality based on the outcome of iterative cardinality (comparison) judgments.





Regions in blue are common to dot-ordering and dot-comparison and are derived from the conjunction of contrasts: (DotOrd > Control)  $\cap$  (DotComp > Control). Regions in red showed greater activity for dot-ordering relative to dot-comparison (DotOrd > DotComp). Voxels in purple are the overlap of the conjunction and difference contrasts from above.

The right IPSa regions was also noteworthy in that it showed overlap for cardinal processing of symbolic and nonsymbolic numbers at the whole brain level (conjunction of NumComp>Control, DotComp>Control). In the current study, we have thus shown right IPSa to be involved in processing nonsymbolic ordinality and cardinality (Figure 2.2), and symbolic cardinality (see Figure 2.5c in the main thesis document). If one were to make a case for a region that processes number in a general sense (see, for example, Jacob et al., 2012), right IPSa would be a likely candidate. No parietal regions showed greater activity for the NumOrd task relative to control (luminance ordering), including right IPSa (see Figure 2.5a-b in the main thesis document for details. With respect to the right IPSa, ordinality in symbolic numbers (NumOrd) is the odd man out. If symbolic and nonsymbolic numbers share some common substrates, it is only in a process-specific manner – that is, for cardinal but not ordinal processing. In particular, taken together with the reverse distance-effects shown in Figure 2.2, these neural results are consistent with our hypothesis that ordinality is key to distinguishing symbolic and nonsymbolic number representation.

Note that several of the claims we have made to this point regarding the similarity and dissimilarity of the neural correlates of ordinal and cardinal processing in symbolic and nonsymbolic numbers have been inferred from null-results. Here, we employ representational similarity analysis, RSA – to directly test the relative similarity of distributed patterns of neural activity during ordinal and cardinal processing of symbolic and nonsymbolic numbers (Kriegeskorte et al., 2008). In this method, one correlates the patterns of activity across voxels for two different experimental conditions. The degree of correlation between different pairs of tasks can then be compared to assess the relative degree of voxelwise covariance, or 'similarity'. This lets us directly compare the degree of similarity between ordinal and cardinal processing in symbolic number regions with that in nonsymbolic number regions (including right IPSa; see Figure 2.4 in the thesis document for complete region details). Results showed significantly less similarity between the NumOrd and NumComp tasks than the DotOrd and DotComp tasks (*p*<.001; black bars in Figure 2.5b of the thesis document). RSA results thus allow us to argue directly from a positive result that ordinal and cardinal processing are less strongly linked in symbolic relative to nonsymbolic numbers. The RSA results both parallel and augment the whole-brain contrast results discussed in previous sections.

Chapter 2 demonstrates that the manner in which ordinality is processed depends strongly on whether numbers are represented symbolically or nonsymbolically. For nonsymbolic numbers, ordinality appears to operate in a manner similar to cardinality. That is, ordinality can be assessed in nonsymbolic numbers, but there does not appear to be a specialized mechanism for doing so. For symbolic numbers, ordinality and cardinality are processed qualitatively differently, indicating that symbolic number representation is highly sensitive to computational context. Our results are consistent with the view that ordinality plays a key role in determining the meaning of symbolic numbers, and, more broadly, that symbolic numbers derive their meaning from a computationally flexible network of associations (Delazer & Butterworth, 1997; Nieder, 2009). In the next chapter, we test the functional relevance of ordinal associations in terms of their relation to individual differences in complex mental arithmetic ability.

### **Chapter 3 Summary**

In Chapter 3 (Lyons et al,. 2011), we show that symbolic number ordering ability mediates the relation between individual variation in one's sense of nonsymbolic number (commonly referred to as the ANS) and more complex math abilities. Work with children and young teenagers has shown a positive relationship between individual differences in nonsymbolic number-acuity (i.e., the ability to discriminate nonsymbolic quantities) and math achievement (e.g., Halberda et al., 2008; Gilmore et al., 2010; Piazza et al., 2010). However, there is a large explanatory gap between knowing that about 10 monkeys is more than about 5 monkeys and the ability to apply complex arithmetic algorithms over abstract symbols to arrive at an exact numerical answer to problems one has never seen before (Nieder & Dehaene, 2009). In other words, considerable work is needed to characterize the intermediary steps between ANS representation and a functioning grasp of complex mental-arithmetic.

We propose that representing relative order in numerical symbols may serve as an ideal stepping stone between the ANS and higher math abilities (e.g., complex arithmetic skills; Figure 3.1a). If the ANS is linked to acquisition of symbolic numerical order, then greater ANS acuity (Figure 3.1b) should be related to more efficient assessment of ordinal relations in symbolic numbers. Moreover, if ordinal understanding in numerical symbols serves as a foundation for the associations accessed during mental arithmetic, then assessment of ordinal relations in symbolic numbers (Figure 3.1c) should predict complex mental-arithmetic ability. Finally, we directly tested our proposal that relative order in numerical symbols is a stepping stone between the ANS and higher math abilities by formally assessing whether the level of one's numerical symbol-ordering ability mediates (explains) the previously observed relation between ANS acuity and more complex math abilities (e.g., Halberda et al.).





**[a]** Examples of the complex mental-arithmetic tasks used to estimate mental-arithmetic ability (dependentmeasure). **[b]** Error rates from the dot-comparison task were used to estimate individual differences in participants' ANS acuity (predictive-measure). **[c]** The numeral-ordering task was used to estimate symbolic number-ordering ability (predictive-measure).

First, we replicated the finding that better ANS acuity predicts math ability. Higher acuity was related to better mental-arithmetic performance (higher mental-arithmetic scores) [r(52)= -.339, p=.012]. Second,

we tested the hypothesis that symbolic number-ordering ability predicts mental-arithmetic performance. Better performance on the numeral-ordering task was significantly correlated with better mentalarithmetic performance [r(52)= -.703, p<.001]. This relation remained significant even when controlling for ANS acuity, performance on numeral-comparison, letter-ordering, working-memory and numeralrecognition tasks (Table 3.1). It is the processing of numerical ordinal information – over and above these factors – that is the key property linking the numeral-ordering and mental-arithmetic tasks. We also controlled for ordering ability in a non-numerical (letter) context, which narrows the result to understanding ordinal relations among symbolic numbers and not ordinal processing in general.

Third, we showed that ANS acuity was positively related to numeral-ordering ability [r(52)=.408, p=.002], a finding in keeping with the view that relative numerical order in symbols may at one time have been derived in part from quantity representation in the ANS (Lyons & Beilock, 2009). These three results can thus be arranged in a potential mediation model which is graphed in Figure 3.2). Results from the mediation analysis were consistent with our main hypothesis: the relation between ANS acuity and complex mental-arithmetic performance (c) was fully mediated by symbolic number-ordering ability (the *ab* path). This was true even when controlling for all covariate factors shown in Table 3.1.

## Table 3.1

Predictor	β ( <i>se</i> )	t (p)	<b>r</b> <sub>partial</sub>	r (p)
NumOrd	7124 (.1568)	-4.543 (<.001)	552	703 (<.001)
<b>ANS Acuity</b>	2308 (1.6014)	144 (.886)	021	339 (.012)
NumComp	.0217 (.1350)	.161 (.873)	.023	305 (.025)
LettOrd	0190 (.1490)	128 (.899)	019	382 (.004)
WorkMem	.0085 (.0044)	1.945 (.058)	.273	.305 (.025)
NumRecog	0004 (.0004)	998 (.324)	144	299 (.028)
Constant	0069 (.6144)			

Table 3.1 shows mental-arithmetic ability (higher number = better performance) regressed on several individual-difference variables: *NumOrd*: numeral-ordering (lower number: better performance), *ANS acuity* (lower number: better acuity), *NumComp*: numeral-comparison (lower number: better performance), *LettOrd*: letter-ordering (lower number: better performance), *WorkMem*: working-memory capacity (higher number: higher capacity), *NumRecog*: numeral-recognition (lower number: better performance). Overall model fit: adj.  $R^2$ =.514. The rightmost column indicates simple Pearson correlation coefficients (and associated *p*-values) between each predictor and mental-arithmetic ability in the absence of any of the other predictors; *r*<sub>partial</sub>, by contrast, is the *r*-value between a given predictor and mental-arithmetic ability and the predictor in question.

## Figure 3.2



In a mediation framework, one asks whether there is a significant indirect effect (quantified as the product of the unstandardized path coefficients, a and b) of the mediator (numeral-ordering) that accounts for some portion of the direct effect c originally observed between the original predictor (ANS acuity) and the outcome (mental-arithmetic) variables. The remaining (unmediated) direct effect is denoted c'. Note that, in this framework, the model is constrained by the assumption that c = ab+c'. Unlike in a standard multiple regression analysis, we are explicitly asking what portion of the *relation between* ANS acuity and mental-arithmetic can be accounted for by the mediating variable (numeral-ordering). Results indicate full (ab is significant but c' is not) as opposed to partial (when both ab and c' remain significant) mediation.

# CONCLUSION

In sum, my thesis shows that efficient representation of ordinal information in symbolic numbers (e.g., Indo-Arabic numerals) is a crucial link between one's fundamental sense of quantity and more complex mathematics. In Chapter 1, I show that the meaning of symbolic numbers is less strongly tied to this sense of quantity (or one's approximate number system, ANS) than has been previously assumed. In Chapter 2, using a combination of behavioral and neural evidence, I show that relative order is processed in fundamentally different ways for symbolic and nonsymbolic (ANS) numbers. Ordinality is thus a key property that distinguishes symbolic from nonsymbolic number representation. In Chapter 3, I show that one's ability to assess ordinal relations in symbolic numbers predicts one's complex mentalarithmetic ability. Furthermore, one's numerical symbol-ordering ability mediates (explains) the previously observed relation between ANS ability and more complex math abilities. Relative order in numerical symbols is a stepping stone between the ANS and higher math abilities. To reach these conclusions, my thesis draws upon multiple methodologies and literature from a wide range of disciplines, including animal neuroscience, cognitive neuroscience in humans, computational modeling, and multiple behavioral domains including developmental research and work with adults. This work also has direct implications for both developmental and educational domains of cognitive science, which are being pursued by multiple research teams. My dissertation has already influenced and is continuing to influence research across several domains and disciplines, and is thus very well aligned with the goals and principles of the Robert J. Glushko Dissertation Prize in Cognitive Science.

### REFERENCES

- Agrillo C, Piffer L, Bisazza A, Butterworth B (2011). Evidence for two numerical systems that are similar in humans and guppies. *PLoS One*, 7:e31923.
- Ansari D (2008). Effects of development and enculturation on number representation in the brain. *Nature Reviews Neuroscience*, 9:278-291.
- Beilock SL, Lyons IM, Mattarella-Micke A, Nusbaum HC, Small SL (2008). Sports experience changes the neural processing of action language. *Proc Natl Acad Sci USA*, 105:13269-13273.
- Buckley PB, Gillman CB (1974). Comparisons of digits and dot patterns. *Journal of Experimental Psychology*, 103:1131-1136.
- Cordes S, Brannon EM (2008). Quantitative competencies in infancy. Developmental Science, 11:803-808.
- Crutch SJ, Warrington EK (2010). The differential dependence of abstract and concrete words upon associative and similarity-based information: Complementary semantic interference and facilitation effects. *Cognitive Neuropsychology*, 27:46-71.
- Damian MF (2004). Asymmetries in the processing of Arabic digits and number words. *Memory and Cognition*, 32:164-171.
- Deacon T (1997). *The Symbolic Species: The Co-Evolution of Language and the Human Brain.* London: Norton.
- Dehaene S, Piazza M, Pinel P, Cohen L (2003). Three Parietal Circuits for Number Processing. *Cognitive Neuropsychology*, 20:487-506.
- Dehaene S (2008). Symbols and quantities in parietal cortex: Elements of a mathematical theory of number representation and manipulation. In Haggard, P & Rossetti, Y (Eds.) Sensorimotor Foundations of Higher Cognition (Attention and Performance) (pp. 527-74), Oxford University Press: New York.
- Delazer M, Butterworth B (1997). A dissociation of number meanings. *Cognitive Neuropsychology*, 14:613–636.
- Gilmore CK, McCarthy SE, Spelke ES (2010). Non-symbolic arithmetic abilities and mathematics achievement in the first year of formal schooling. *Cognition*, 115:394-406.

- Halberda J, Mazzocco MM, Feigenson L (2008). Individual differences in non-verbal number acuity correlate with maths achievement. *Nature*, 455:665-668.
- Hyde DC, Spelke ES (2011). Neural signatures of number processing in human infants: evidence for two core systems underlying numerical cognition. *Developmental Science*, 14:360-371.
- Kriegeskorte N, Mur M, Bandettini P (2008). Representational similarity analysis connecting the branches of systems neuroscience. *Frontiers in Systems Neuroscience*, 2:4.
- Lyons IM, Beilock SL (2009). Beyond quantity: individual differences in working memory and the ordinal understanding of numerical symbols. *Cognition*, 113:189-204.
- Lyons IM, Mattarella-Micke A, Cieslak M, Nusbaum HC, Small SL, Beilock SL (2010). The role of personal experience in the neural processing of action-related language. *Brain Lang*, 112:214-222.
- Lyons IM, Beilock SL (2011). Numerical ordering ability mediates the relation between number-sense and arithmetic competence. *Cognition*, 121:256-261.
- Lyons IM, Ansari D, Beilock SL (2012). Symbolic Estrangement: Evidence Against a Strong Association Between Numerical Symbols and the Quantities They Represent. *Journal of Experimental Psychology: General*, 141:635-641.
- Lyons IM, Beilock SL (2012a). Mathematics anxiety: separating the math from the anxiety. *Cereb Cortex*, 22:2102-2110.
- Lyons IM, Beilock SL (2012b). When math hurts: math anxiety predicts pain network activation in anticipation of doing math. *PLoS ONE*, 7:e48076.
- Merten K, Nieder A (2009). Compressed scaling of abstract numerosity representations in adult humans and monkeys. *Journal of Cognitive Neuroscience*, 21:333-346.
- Nieder A (2005). Counting on neurons: The neurobiology of numerical competence. *Nature Reviews Neuroscience*, 6:177-190.
- Nieder A (2009). Prefrontal cortex and the evolution of symbolic reference. *Current Opinion in Neurobiology*, 19:99-108.
- Nieder A, Dehaene S (2009). Representation of number in the brain. *Annual Review of Neuroscience*, 32:185-208.
- Piazza M, Izard V, Pinel P, Le Bihan D, Dehaene S (2004). Tuning curves for approximate numerosity in the human intraparietal sulcus. Neuron, 44:547-555.
- Piazza M, Facoetti A, Trussardi AN, Berteletti I, Conte S, Lucangeli D, Dehaene S, Zorzi M (2010). Developmental trajectory of number acuity reveals a severe impairment in developmental dyscalculia. *Cognition*, 116:33-41.
- Santens S, Roggeman C, Fias W, Verguts T (2010). Number processing pathways in human parietal cortex. *Cerebral Cortex*, 20:77-88.
- Verguts T, Fias W (2004). Representation of number in animals and humans: a neural model. *J Cogn Neurosci*, 16:1493-1504.
- Wiese H (2003). Iconic and non-iconic stages in number development: The role of language. *Trends in Cognitive Sciences*, 7:385-390.