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# Development of common neural representations for distinct numerical problems

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ABSTRACT

How the brain develops representations for abstract cognitive problems is a major unaddressed question in neuroscience. Here we tackle this fundamental question using arithmetic problem solving, a cognitive domain important for the development of mathematical reasoning. We first examined whether adults demonstrate common neural representations for addition and subtraction problems, two complementary arithmetic operations that manipulate the same quantities. We then examined how the common neural representations for the two problem types change with development. Whole-brain multivoxel representational similarity (MRS) analysis was conducted to examine common coding of addition and subtraction problems in children and adults. We found that adults exhibited significant levels of MRS between the two problem types, not only in the intraparietal sulcus (IPS) region of the posterior parietal cortex (PPC), but also in ventral temporal–occipital, anterior temporal and dorsolateral prefrontal cortices. Relative to adults, children showed significantly reduced levels of MRS in these same regions. In contrast, no brain areas showed significantly greater MRS between problem types in children. Our findings provide novel evidence that the emergence of arithmetic problem solving skills from childhood to adulthood is characterized by maturation of common neural representations between distinct numerical operations, and involve distributed brain regions important for representing and manipulating numerical quantity. More broadly, our findings demonstrate that representational analysis provides a powerful approach for uncovering fundamental mechanisms by which children develop proficiencies that are a hallmark of human cognition.

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## 1. Introduction

How are abstract problems represented in the brain? How do experience and development shape neural representations for abstract problems? The answers to these questions are crucial for understanding the neural basis of skill acquisition and cognitive development. The internalized representation of problem solutions has long been debated with arguments for decontextualized abstracted solution representations, non-abstract context-dependent processes or even hybrid views, as best exemplified by models in the domain of numerical problem solving (Campbell, 1994; Dehaene et al., 2004; McCloskey, 1992). Characterizing the developmental profile of neural representations associated with efficiently processing strings of abstract symbols can provide new insights into the nature of the underlying code for these processes. While localization of brain activation has provided useful knowledge about the relative engagement of task-specific brain areas during problem solving, they offer limited insights into the cognitive and neural representations of distinct numerical problems in the brain. Here we use novel multivoxel representational similarity (MRS) analyses to investigate how neural representations for abstract problems are formed and mature after more than a decade of experience with problem solving.

We tackle this fundamental question using numerical problem solving, a cognitive domain crucial for academic skill development. Foundational math problem solving skills contribute to proficiency in a wide range of contexts from advanced scientific and engineering reasoning, to more simple quantitative operations

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important for daily life (Butterworth et al., 2011; Geary, 2013; Geary et al., 2013). Converging evidence from infants, children and adults as well as non-human primates suggests that representation of quantity is a foundational ability for numerical problem solving tasks ranging from simple number comparisons to complex arithmetic (Ansari and Dhital, 2006; Cantlon and Brannon, 2006; Cohen Kadosh et al., 2008; Dehaene et al., 2003; Izard et al., 2009; Simon, 1997, 1999; Soltesz et al., 2010; Xu and Spelke, 2000). This ability is supported by multiple brain areas including the intraparietal sulcus (IPS) in the dorsal posterior parietal cortex (PPC), the fusiform gyrus (FG) in the ventral temporal–occipital cortex (VTOC), and prefrontal cortex (PFC; Ansari and Dhital, 2006; Arsalidou and Taylor, 2011; Cantlon and Brannon, 2006; Cohen Kadosh et al., 2008; Houde et al., 2010; Menon et al., 2000; Wu et al., 2009). Normative developmental neuroimaging studies in children and adults have shown that there is decreased dependence on the PFC and greater reliance on the IPS and other subdivisions of the PPC with experience and learning (Ansari and Dhital, 2006; Cantlon et al., 2006, 2009; Kawashima et al., 2004; Rivera et al., 2005). Similar to the IPS, activity levels in VTOC, including the FG, also increase with age during numerical problem solving (Rivera et al., 2005). Beyond this frontal to posterior shift in the locus of activation, little is understood about how the brain builds representations for numerical problems during development.

Among the functional circuits implicated in numerical problems, current cognitive models have suggested different representations in posterior brain areas, with perceptual representations supported by visual number form processing within the VTOC, whereas the parietal cortex is thought to support semantic representations and manipulation of quantity along a mental number line (Ansari, 2008; Arsalidou and Taylor, 2011; Cantlon et al., 2009; Cohen Kadosh et al., 2008; Dehaene et al., 2003; Holloway et al., 2013). Consistent with this view, one cross-linguistic fMRI study found that perceptual processing of digits and ideographs was associated with activation in the FG whereas semantic processing of both symbol types was associated with modulation of IPS activation (Holloway et al., 2013). Critically, these models of information processing are mainly based on studies in adults, and thus, their relevance to the understanding of maturing representations in the developing brain remains unclear. An important unresolved question is whether children and adults have similar representations in the IPS and FG, two brain areas important for different aspects of abstract numerical problem solving (Cantlon et al., 2009; Holloway et al., 2013; Rivera et al., 2005).

To investigate the maturation of brain representations for abstract numerical problems we focused on addition and subtraction, two complementary arithmetic operations that manipulate the same quantity in opposite directions. In elementary school curriculum, addition is learned as the primary operation whereas subtraction builds upon prior knowledge of addition and its inverse relationship with addition (Campbell, 2008). Behavioral studies have characterized distinctive strategies used to solve these arithmetic operations at different developmental stages. School-age children, particularly 3rd graders, apply retrieval strategies to solve addition problems 65% of the time, while only 19% of subtraction problems are solved using this strategy (Barrouillet et al., 2008). In contrast, adults solve 76% of addition problems by retrieval and still use this strategy during subtraction 58% of the time (Campbell and Xue, 2001). These differences in retrieval rates suggest that with development, there is a shift from effortful counting to automatic fact retrieval, leading to a convergence of problem solving strategies across the two operations.

Voxel-based univariate analyses have provided evidence for both distinct and overlapping brain responses across arithmetic operations (De Smedt et al., 2011; Fehr et al., 2007; Kawashima et al., 2004; Rosenberg-Lee et al., 2011). However, no consensus has yet emerged for how addition and subtraction are represented in the brain. Critically, nothing is known about the similarities in neural representations for the two types of distinct numerical problems and how they mature with development. Common representations are a powerful approach for examining abstract coding of perceptual objects and semantic categories independent of low-level features (Edelman, 1998). In the perceptual domain, common, invariant, representations play a fundamental role in object recognition and categorization (Biederman, 1987). While some progress has been made in identifying brain areas that support object invariance in perceptual domains (Drucker and Aguirre, 2009), little is known about the nature of common representations for abstract numerical problems.

Multivariate pattern analysis is uniquely suited to addressing important unaddressed questions related to neural representations for distinct numerical problems. MRS analysis probes the spatial correlation in activity patterns associated with distinct stimuli and can provide novel insights into information processing that are often missed by conventional methods which emphasize localization of brain responses (Kriegeskorte et al., 2008; Mur et al., 2009). Although MRS has been primarily used in studies of low-level visual perception (Connolly et al., 2012; Kriegeskorte et al., 2008; Mur et al., 2009; Said et al., 2010), an emerging literature is beginning to suggest that it is also a promising tool for probing higher cognitive functions (Ashkenazi et al., 2012; Blair et al., 2012; Ezzyat and Davachi, 2014; Gagnepain et al., 2014; LaRocque et al., 2013; Prado et al., 2011; Qin et al., 2014; Xue et al., 2013, 2010). For example, Xue and colleagues reported that greater MRS across repetitions of an item was associated with higher rates of subsequent memory recall in adults (Xue et al., 2010). In this study, we use a whole-brain MRS approach to probe the common neural representations for distinct numerical problems in young children and adults.

We acquired fMRI data from 28 adults (ages 19–22) and 28 children (ages 7–10) while they solved single-digit addition and subtraction problems. We implemented a novel whole-brain analysis to first investigate MRS across the two operations in each group and then examined age-related differences by contrasting MRS between adults and children. MRS has been primarily implemented using a region of interest (ROI) approach to probe cognitive function in predefined regions (Ashkenazi et al., 2012; Blair et al., 2012; Kriegeskorte et al., 2008; Prado et al., 2011; Said et al., 2010; Xue et al., 2010). Limitations of this approach include the restricted brain areas examined and biases inherent in selection of regions-of-interest (ROIs; Fox, 1991; Kriegeskorte et al., 2009; Vul et al., 2009). Searchlight methods, which span the entire brain, can overcome these limitations (Connolly et al., 2012; Devereux et al., 2013; Qin et al., 2014; Rothlein and Rapp, 2014; Xue et al., 2013) and offer a powerful technique to investigate how learning and development shape neural representations across multiple brain areas. To contrast age-related differences in VTOC areas associated with visual number form versus dorsal parietal areas associated with semantic representation of quantity (Ansari, 2008; Arsalidou and Taylor, 2011; Cohen Kadosh et al., 2008; Dehaene et al., 2003), here we also examine MRS in cytoarchitectonically-defined subdivisions of the PPC and VTOC.

Based on the behavioral studies reviewed above, which have pointed to convergence of problem solving strategies for addition and subtraction with development (Barrouillet et al., 2008; Campbell and Xue, 2001), we predicted that adults would show more similar neural representations across addition and subtraction problems in core brain areas implicated in arithmetic problem solving. Statistically significant levels of MRS during addition and subtraction problem solving would provide evidence for common