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The emergence of a brain network for numerical thinking

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Abstract

Educated adults and children engage a network of frontal and parietal brain regions for numerical thinking. Recent studies document some prominent changes as this network emerges over development, including a unilateral right to bilateral shift in number-selective parietal brain activity, a strengthening of intra- and inter-hemispheric parietal connections, reduced engagement of prefrontal regions, and decoupling between prefrontal and parietal regions. Based on these findings, it appears that right parietal regions form an innate or early emerging basis for representing numerical magnitudes, whereas the left parietal regions support representation of culturally acquired symbolic numbers that begin to emerge over childhood. Functional connections between parietal hemispheres and parietal and prefrontal cortex likely support associations between magnitudes and symbols, as they are associated with numerical proficiency. Prefrontal regions appear to provide general cognitive resources to support these associations, engaging and positively correlating during the learning process and disengaging and negatively correlating after mastery.

A mature brain network for numerical thinking

Educated human adults and older children reliably engage a network of brain regions in the frontal and parietal lobes for numerical cognition, including bilateral regions of the inferior and superior parietal lobules, as well as middle and inferior frontal cortex (see Dehaene et al., 2003; Nieder & Dehaene, 2009; Sokolowski et al., 2016).^{1,2}

Central to the mature numerical cognition network are bilateral portions of the interparietal sulcus (IPS). The IPS is a surface groove that divides the inferior and superior portions of the multifunctional parietal cortex, portions of which show a degree of specialization for numerical thinking (see Figure 1). That is, particular IPS regions selectively activate for numerical tasks and are sensitive to the numerical content or meaning of a target stimulus over and above their sensitivity to other non-numerical properties of it like size, shape, or color (Dehaene et al., 2003; Nieder & Dehaene, 2009).³ Furthermore, overlapping IPS regions respond similarly to numerical information across formats, including non-symbolic arrays of objects and symbolic digits (Sokolowski et al., 2016; Wilkey et al., 2020). Permanent damage to these particular IPS regions impairs numerical abilities, transcranial magnetic stimulation (TMS) temporarily alters numerical thinking, and functional activation in this region is markedly different in individuals with a mathematics learning disability (Faye et al., 2019; Kucian, 2016).

¹ Here I discuss the emergence of the numerical cognition network and, as such, my literature review attempts to focus on studies of early developing non-symbolic numerical and symbolic number processing and avoid studies of later developing arithmetic or higher-order mathematics which go beyond my proposed purpose and scope.

² A ventral portion of the inferior temporal gyrus, referred to as the number-form area, is also reliably seen to engage, possibly selectively, in contexts where visual numerals are present (see Hannagan et al., 2015).

³ There is continued debate about the degree of specialization for numerical processing in IPS and the experimental conditions under which it breaks down (see Leibovich et al., 2017).

The predominate theoretical model of number representation in the brain, the triple-code model (Dehaene et al., 2003) posits that, in addition to number-specific IPS representing abstract numerical magnitudes, two other parietal regions allow for numerical representation in other formats (Figure 1). More inferior parietal regions of the angular gyrus (AG) are proposed to represent numbers in verbal form and posterior superior parietal lobule regions (PSPL) are proposed to link numerical processing with spatial processing and attention (see Dehaene et al. 2003). Number-sensitive regions in the angular gyrus respond more during numerical tasks that involve language or symbols compared to numerical tasks that do not involve symbols (Arsalidou & Taylor, 2011; Price & Ansari, 2011). However, the angular gyrus also responds in non-numerical contexts involving language or symbol processing more broadly, suggesting that it is not number-specific and, instead may support associations of numerical meaning with language and symbols (see Seghier, 2013). More posterior regions of the superior parietal lobule (PSPL) are thought to link numerical thinking to visuospatial attentional processing. These regions activate for a wide range of numerical tasks, but also seem to be engaged in non-numerical tasks requiring the orienting and maintenance of attention to space such as those involving eye-movements, covert attentional orienting to space, pointing, spatial working memory, and mental rotation (see Dehaene et al., 2003). Given the overlap in activation for numerical and non-numerical tasks, functional activity in posterior superior parietal regions during numerical thinking is also better characterized as supplementally linking numerical representation to symbolic and spatial representation rather than being number-specific.

Finally, frontal and prefrontal cortical regions including portions inferior frontal cortex (IFC), insula, anterior cingulate cortex (ACC), dorsolateral prefrontal cortex (DLPFC), and precentral gyrus broadly known to be involved in planning, reasoning, and decision making, are

also reliability engage for numerical tasks, (see Kersey & Cantlon, 2017a; Arsalidou et al., 2018). Although the precise role of prefrontal regions in numerical thinking is contested, the dominate view is that they also play a supportive role in linking numerical representation-specific nodes with language, semantic, and symbol systems (e.g., Cantlon et al., 2009; Nieder, 2009).

Developmental Origins

Together the literature briefly reviewed provides a clear and consistent picture of which regions are reliability engaged and the proposed functional role they likely play in numerical thinking in the mature brain. However, most human adults or children who participate in neuroimaging studies have had years of cultural experience (i.e, instruction and practice) with numbers, obtaining a high degree of expertise in numerical thinking. Thus, these studies do not provide much insight into *how* this brain network emerges, which aspects are continuous, which develop, and what factors drive their emergence. To answer these questions, we must turn to studies with younger developmental populations at ages before substantial informal or formal experience with symbolic numbers occurs. Developmental neuroimaging data on the issue are more limited for a number of reasons, including a host of practical constraints on neuroimaging data collection with young children. For example, neuroimaging measures most often require more set-up time, more invasive procedures, and additional constraints on participant movement compared to behavioral measures alone. Despite these sorts of challenges, a substantial body of evidence has now accrued, suggesting several consistent developmental patterns that give rise to this network. In turn, this developmental work is also beginning to provide novel insights into function of the different brain regions in the numerical cognition network and holds promise for translating neuroscience into practice.

Early-selectivity suggests right IPS foundation

Children, like adults (Piazza et al., 2004), do show selective engagement of IPS regions for symbolic and non-symbolic numerical processing (see Kersey & Cantlon, 2017a). For example, Cantlon and colleagues (2006) showed that the IPS in children as young as 4 years of age responds to changes in the number of objects in visually presented arrays, but not to changes in the shape (and other varying dimensions) of the objects. Like adults, parietal regions that respond to non-symbolic number eventually overlap with those that respond to symbolic number in children (e.g., Cantlon et al., 2009; Holloway & Ansari, 2010). The IPS response to symbolic and non-symbolic numbers can be further dissociated from processing of people and words (and shapes) in children 4-11 years old who are in the midst of mastering the symbolic number system (e.g., Emerson & Cantlon, 2012). Furthermore, individual differences in numerical sensitivity of the IPS are related to behavioral numerical abilities and reduced IPS activation is associated with dyscalculia, a mathematics-specific learning disability (e.g., Price et al., 2007). These results highlight the evidence that IPS shows some degree of specialization for numerical processing by around 4 years of age and suggest that activity in IPS is fundamentally related to numerical thinking and learning over development. However, even before formal schooling starts, children as young as 3-4 years growing up in modern cultures also have substantial experience, direct instruction (albeit mostly informal) with, and a basic understanding of symbolic numbers (see Wynn, 1992). Thus, even from the child neuroimaging data reviewed above, the origin of parietal sensitivity and specialization for number processing, including individual differences, is still unclear: it could emerge from experience with symbolic numbers, number language, counting practice, or it could precede it and be largely genetically determined.

A majority of human neuroimaging work mentioned above has been carried out using functional magnetic resonance imaging (fMRI), which manipulates the magnetic fields around the head and measures resulting biophysical changes to image brain structure and infer brain activity. Collecting fMRI data with children younger than 3-4 years of age not yet widely feasible due to necessary constraints on movement and attention. More specifically, fMRI requires participants to lay alone, supine in the hollow bore of magnet and remain motionless (or as close to as possible) as scans are acquired. A few studies have employed an alternative neuroscience measure, functional near-infrared spectroscopy (fNIRS), to study numerical processing in infants. FNIRS is a non-invasive optical method that estimates changes in the hemodynamic response of the brain from measures light intensity projected to brain tissue from the scalp (see Gervain et al., 2011). FNIRS allows the brain response to be measured through headgear placed on the scalp, tolerating some degree of natural movement even while a child sits on a caregiver's lap (Gervain et al., 2011). It should be noted that the spatial resolution of fNIRS is a few centimeters (usually 2-3 cm), about an order of magnitude more coarse than fMRI. Thus, it may be limited in testing hypotheses when more fine-grained distinctions between adjoining brain regions are required.

Using fNIRS, several studies have now demonstrated that right IPS regions are sensitive to and may be selective for processing numerical information within the first year of life (Edwards et al., 2016; Hyde et al., 2010). For example, one study by Hyde and colleagues (2010) showed that the right IPS responds selectively to changes in the number of objects presented but not to changes in the shape of the objects in 6-month-old infants using a similar numerical adaptation paradigm as has been used in fMRI studies of adults and children (Cantlon et al., 2006; Piazza et al., 2004). A follow-up fNIRS study replicated and extended these results,

showing numerical sensitivity of the right IPS could be further dissociated from more general visual attentional processing in 6-month-old infants (Edwards et al, 2016, see supplemental materials, S1). Although only a few infant neuroimaging studies with relatively small samples have been done, these double dissociations suggest a striking degree of specialization of the IPS for numerical processing within the first year of life that cannot be explained by symbolic number instruction or experience with counting objects.

Unilateral to bilateral parietal shift suggests distinct hemispheric functions

Interestingly, existing studies with infants show only right-lateralized sensitivity to numerical information (Edwards et al., 2016; Hyde et al., 2010). By 4 years of age, there is evidence of some bilateral numerical selectivity, even though right-lateralized response is stronger (e.g., Cantlon et al., 2006; Riviera et al., 2005). Bi-lateralization, characterized by an increase in number-selective activity in left-lateralized IPS, appears to increase with age during childhood until eventually both the left and right IPS respond selectively to non-symbolic and symbolic numbers (e.g., Ansari, 2008; Cantlon et al., 2006; Piazza et al., 2004; see supplemental materials, S2). Right-lateralized number-related IPS activity appears to be stable, correlated longitudinally over childhood, and continually related to perceptual acuity in non-symbolic numerical discrimination (Emerson & Cantlon, 2014; Kersey & Cantlon, 2017b). In contrast, the left IPS does not appear to be number-selective early in infancy (Edwards et al., 2015). Selectivity for numerical processing in left IPS emerges over development and, while not correlated longitudinally, changes in left IPS number-selectivity are related to gains in conceptual understanding and behavioral competency (see Emerson & Cantlon, 2014). These data clearly suggest different functional roles for the left and right IPS in numerical thinking over development.

Given bi-lateralization roughly coincidences with the introduction of symbolic system around age 2-5 years (see Wynn, 1992), several clear hypotheses emerge. For all, right lateralized IPS regions are hypothesized to initially support processing of non-symbolic approximate numerical magnitudes. One possibility is that left-lateralized IPS regions become involved in numerical thinking by supporting the representation verbal-symbolic numbers (Ansari, 2008; Holloway et al., 2010; Holloway et al., 2013), with left-lateralized activity emerging as symbolic number experience is acquired. Another possibility is that left-lateralized IPS supports the representation of an exact cardinal values, with conceptual competency with exact number concepts rather than linguistic or symbolic number experience alone driving the emergence of left-lateralized numerical selectivity. Still another possibility that is not mutually exclusive is that the emergence of left-lateralized number-selective IPS activity results from brain maturation in early childhood, either as a result of left IPS maturation itself or increasing connectivity between left IPS and the already number-selective right IPS (Damoiseaux and Greicius, 2009; Supekar et al., 2010). In this case, bi-lateralization would be related to age over and above individual differences in experience or conceptual mastery. Identifying hemispheric differences in IPS function is challenging in numerate children and adults because at some point early in development overlapping bilateral IPS regions respond to both non-symbolic and symbolic number notations (e.g., words, digits, dots) (see Kersey & Cantlon, 2017a). Engaging one is likely to automatically engage the other. Furthermore, experience, conceptual mastery, and brain maturation are likely correlated, making it necessary to measure and control for each when attempting to distinguish between hypotheses. Critical to future work will be to investigate how lateralization and function of the IPS changes between infancy and the acquisition of numeracy.

Contextual prefrontal engagement suggests support for learning

Engagement of prefrontal cortex ,including IFG, DLPFC, ACC, and the insula, has also been documented in numerical tasks in child as has been seen in adults (see Kersey & Cantlon, 2017a). Unlike the parietal regions, younger children seem to engage some prefrontal regions to a greater extent than older children and adults when processing numerical information (e.g., Ansari et al., 2005; Cantlon et al., 2009; Emerson & Cantlon, 2014; Figure 2). A recent meta-analysis showed greater activation in IFG, DLPFC, and ACC for numerical tasks in children compared to adults (see Kersey & Cantlon, 2017a). However, the pattern of decreasing prefrontal activation appears to be more nuanced than a negative correlation with age or maturation. That is, prefrontal engagement for numerical cognition is highly dependent on context (see Kersey & Cantlon, 2017a for review). For example, children show greater prefrontal activation for tasks involving emerging symbolic skills compared to non-symbolic tasks or compared to passive tasks (see Kersey & Cantlon, 2017a). In addition, some prefrontal activity (including insula, and ACC) is related to trial-by-trial reaction times in numerical tasks in children, suggesting a link between effort on a particular trial and prefrontal engagement (Emerson & Cantlon, 2014). Furthermore, adults seem to show patterns of prefrontal activation similar to young children when they are presented with harder numerical or mathematical tasks (e.g., cross-notation comparison task) (see Emerson & Cantlon, 2014). Number-selectivity does not increase in prefrontal regions over development like it does in IPS and instead, changes in response to number follows similar trends as changes in response to other sorts of stimuli (Emerson & Cantlon, 2014).

Some have characterized the contrast between reduced prefrontal engagement and increased parietal activation over development as a fronto-parietal shift, given the observation

that both appear to occur during development (Ansari, 2008; Nieder & Dehaene, 2009).

However, the new contextual evidence from developmental neuroimaging reviewed above suggests a simpler alternative: reduced activity over development is due to a decreased reliance on prefrontal brain regions (and the general cognitive resources they underlie) that may tend to correlate with are not tethered to increases in parietal activation and specialization. Broadly speaking, then, it seems that prefrontal engagement is seen in the context of learning, allowing access to general cognitive resources needed to make new associations (e.g., between symbols and magnitudes; between symbols formats, between different numerical values or meanings, etc.), and engagement diminishes with proficiency or mastery, rather than purely with age or maturation (Figure 2). The prediction that follows from this interpretation is that when learning demands are high, engagement should be present regardless of age. Prefrontal engagement should be diminished in contexts of conceptual mastery or expertise.

Connecting the numerical cognition network

Studies of how connectivity between nodes in the numerical cognition network first emerge are not yet abundant (see Moeller, Willmes, Klein, 2015) due undoubtedly to the practical limitations of testing young children with relevant MRI methodologies. Nevertheless, several patterns have emerged from the few developmental studies that have been done on numerical processing tasks (and not arithmetic or higher order mathematics). First, functional and structural connections between number-specific brain regions, particularly connectivity within and between parietal hemispheres, have been found to be positively related to numerical abilities and correlated with development (e.g., Cantlon et al., 2011; Park et al., 2013; Park et al., 2014). Second, functional connectivity between number-specific and other general cognitive and/or language systems are also important to competence (see Moeller et al., 2015). For

example, Emerson and Cantlon (2012) report positive correlations between functional connectivity of frontal and parietal nodes and numerical performance in 4-11 years old children.

While a comprehensive review of more abundant connectivity studies related to later developing mathematics is beyond the scope of this paper, it may be important to note that intra- and inter- hemisphere parietal connectivity also continues to show positive correlations with development, while frontal-parietal functional connectivity routinely shows negative correlations with mathematics performance over later development (e.g., Battista et al., 2018). Relatedly, mathematics learning disability has been associated with hyperconnectivity between prefrontal and parietal regions (e.g., Rosenberg-Lee et al., 2015). The reduction in functional coupling between activity in prefrontal and parietal regions over typical development for mathematics has interpreted as interactive specialization through “systems-level pruning” (see Battista et al., 2018). At this point, it is unclear whether a reduction in functional connectivity with development should be interpreted as actual functional reorganization or, more simply, a correlate of reduced engagement of resources for learning with increases in proficiency. A novel prediction that follows from the disengagement hypothesis is that resources will continue to be available when needed for learning and the developmental trajectory of heightened and then reduced prefrontal-parietal functional coupling should repeat itself throughout the lifespan as novel numerical and mathematical skills continue to be acquired.

Summary and Conclusions

In sum, the brain network for numerical cognition has been well-established through studies of numerical and mathematical thinking in mature adults and older children (see Dehaene et al., 2003; Ansari, 2008). Prominent theories (e.g., Dehaene et al., 2003), based largely on data from mature populations, have ascribed precise roles to the nodes and connections in this

network, which appear largely accurate in developmental data (see Kersey & Cantlon, 2017a). However, recent developmental cognitive neuroscience data clearly document several prominent changes in functional brain activity and connectivity that correlate with development and need to be further understood and accounted for in a comprehensive model of numerical cognition in the brain (Figure 3). These included an increase in numerical sensitivity of parietal regions, an increase in parietal engagement associated with a unilateral right to bilateral shift in IPS number-selectivity, the emergence of intra- and inter-hemispheric parietal connections, and reduced engagement of prefrontal regions over development and with increases in numerical competency (Figure 3).

Based on these developmental data, it seems that right IPS regions provide an innate or early emerging basis for thinking about non-symbolic magnitudes. In contrast, number-related activity emerges in left IPS as symbolic numerical cognition emerges, allowing numerical meaning to be represented in various new symbolic forms, including exact number concepts (i.e., natural number). This bi-lateralization, characterized by increased left IPS number-selectivity, should be associated with the development of symbolic number knowledge. Furthermore, associations between formats are facilitated by engagement and connection with prefrontal regions, with prefrontal engagement and connectivity being positively associated of numerical ability in contexts where learning is occurring and negatively associated once concepts become mastered the need for general cognitive resources is less. This process should be seen repeatedly over development as more advanced knowledge of numbers and mathematics are acquired.

A Need to Understand the Mechanisms of Change

While these signatures of network emergence appear to be robust over development, the precise mechanisms that drive them remain unknown. In each case, maturation, number-specific

experience, general cognitive development, mastery, and strategy are all potential mechanisms related to change. More detailed longitudinal and cross-sectional studies are needed, with children before (~infancy-2 years) and during (~2-4 years) acquisition of a symbolic number system, in order to better understand the mechanisms at play. Of key importance will be to collect data on the precise timing of these change, as well concurrent individual-level data on the type of input children are receiving. Input data should include exposure to numerical language, informal and formal number instruction, and broader language experience (e.g., Berkowitz et al., 2015). Concurrent assessments of conceptual understanding are needed to triangulate the relationships between brain changes, experience, and conceptual gains in numerical understanding. With advances in developmental brain measurement, such studies are now feasible to conduct, and we may soon be able to include parallel measures of structure, function, and connectivity. One additional hope is that a better understanding of the emergence of this brain network for numerical thinking may provide new insight into the learning process, allowing us to better align teaching strategy and intervention with our biological toolkit.

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Figure 1.

Figure 1 caption. Posterior brain regions involved in numerical processing in the mature brain (Figure reproduced with permission from Dehaene et al., 2003).

Figure 2.

Figure 2 caption. Network of brain regions engaged in response to number (yellow), reaction times (blue) and the overlap between the two (green) in adults and children. Note that children show more number-related activity (yellow) than adults in IFG/Insula (reproduced with permission from Emerson & Cantlon, 2014).

Figure 3.

Figure 3 Caption. Brain network for numerical thinking. A). Right intraparietal sulcus (R-IPS) is selective for numerical processing from the first year of life. B). Left intraparietal sulcus (L-IPS) becomes number-selective in early childhood. Connections between R-IPS and L-IPS also increase over development C). Several regions in the prefrontal cortex (PFC) engage for numerical processing. Number-related activity in PFC and functional connectivity to parietal regions appear to be positively correlated early in the learning processing and negatively correlated with mastery.

Supplemental materials

Figure S1.

Figure S1. Caption. Infant fNIRS data showing an isolated, right-lateralized parietal response to numerical change in visually presented dot arrays that dissociates from a more general visual-attentional response (Edwards et al., 2017). Numbers on the model head represent location of different data channels on the infant scalp. The red highlighted channel represents the single number-selective channel. The blue highlighted area represents a cluster of channels where a general visual-attentional response was observed. Data figures represent change in oxygenated hemoglobin in channels highlighted at significant channels for different conditions (no change, number change, attentional animations).

Figure S2.

Figure S2 Caption. Functional response to number in the intraparietal sulcus of adults and children as observed by fMRI (Kersey & Cantlon, 2017b). A). IPS regions of interest used. B). Tuning of right and left IPS to number in adults (red dotted line, data from Piazza et al., 2004) and children. Left IPS has more precise tuning to number in adults compared to children. C). A stronger relationship between precision of neural tuning to number in right (red) IPS and behavioral performance on a numerical comparison task compared to left IPS (blue) in children.