Précis of *Preservation and plasticity in the neural basis of numerical thinking in blindness*

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Overview

The role of nature versus nurture in development is an enduring debate in philosophy, psychology and neuroscience. To what degree are the mind and brain shaped by the intrinsic structure of the cortex (as specified by genetics) versus experience? My dissertation sheds light on this debate by using tools from cognitive science and neuroimaging to compare the minds and brains of groups with drastically different sensory experiences: typically developing sighted individuals and blind individuals.

The absence of vision has broad impacts on cognitive function, affecting not only sensory processing but many higher cognitive domains as well. In my dissertation, I studied how the absence of vision modifies the cognitive and neural basis of numerical thinking. Numerical thinking is pervasive in the daily lives of all humans and numerical abilities are predictors of success in modern society. Thus, the developmental origins of numerical cognition is a thriving area of research not only for theoretical, but practical purposes. From birth, vision is a major source of numerical information in our environment. Numerical abilities show strong relationships with visual perception and visuo-spatial abilities (Tibber et al., 2013; Zhou, Wei, Zhang, Cui, & Chen, 2015). Despite these relationships, the role of visual experience in the development of early numerical capacities and their neural bases remains unknown.

Working with blind individuals provides a unique opportunity to ask how drastically different histories of visual experience shape the development of numerical thinking and its neural implementation. In addition to working with this unique population, I combine methods from cognitive science such as psychophysics, as well as several fMRI methods from cognitive neuroscience to gain a more comprehensive understanding of how the cognitive and neural bases of numerical thinking develop in the absence of vision. The findings of this dissertation are relevant to a broad audience of researchers in cognitive science, cognitive neuroscience, development, education, clinical psychology and neuroplasticity.

Chapter 1: Background

Prior to using number symbols to represent quantities and perform mathematical calculations, humans and non-human animals are able to approximate the quantity of items in a set without counting. For example, pre-verbal infants habituate to displays presenting the same number of dots repeatedly but dishabituate when the number of dots on the display changes, even when controlling for non-numerical visual features such as area (Xu & Spelke, 2000). Although this ability seems far from the more sophisticated mathematical abilities of adults, a wealth of evidence demonstrates that numerical approximation and math abilities are correlated across individuals (Halberda, Mazzocco, & Feigenson, 2008). Numerical approximation abilities in infancy have even been shown to predict future number knowledge in childhood (Starr, Libertus, & Brannon, 2013). One hypothesis for these findings is that representations of approximate number are a precursor for symbolic number concepts (Szkudlarek & Brannon, 2017). Consistent with this idea, representations of approximate number and mathematical processing are co-localized in the intraparietal sulcus (IPS) of the cortex (Lussier & Cantlon, 2017).

Despite the importance of these early numerical approximation abilities, we know surprisingly little about their developmental origins. One possibility is that representations of approximate number are formed as a result of visual experience with sets of objects. Quantity is a highly salient and behaviorally relevant feature of visual scenes (Burr & Ross, 2008). Indeed, neural networks trained on visual images of object sets spontaneously develop representations of quantity akin to those found in non-human primates (Stoianov & Zorzi, 2012). Representations of approximate number may analogously develop in the IPS as a result of visual experience with object sets. Although one can experience quantities to some extent through sound and touch, these modalities are much less efficient for conveying numerical information compared to vision. Thus, it is possible that representations of approximate number will be compromised or modified in individuals who have no visual experience.

Alternatively, experience such as vision may not be required for the establishment of approximate number representations. Indeed, representations of approximate number are present in our evolutionary heritage and there is some evidence that infants can perceive small numbers just hours after birth (Izard, Sann, Spelke, & Streri, 2009; Viswanathan & Nieder, 2013). In this dissertation, I directly adjudicate between these alternatives by asking whether the cognitive and neural basis of numerical thinking is modified in individuals with drastically different visual experiences.

Chapter 2: Precision of approximate number system (ANS) and its link to the symbolic number system develop independent of visual experience

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I begin by asking whether atypical sensory experiences alter symbolic and non-symbolic numerical abilities at the level of behavior. I worked with individuals who have been blind from birth and have no cognitive or neurological disabilities. To recruit a sample size of congenitally blind individuals that is larger than what is typically reported in the literature, we worked with the National Federation of the Blind to conduct part of this study at their annual convention, which hosts hundreds of blind attendees.

Twenty-four congenitally blind and 15 age- and education-matched sighted individuals completed an extensive battery of standardized cognitive tests. Standardized testing was conducted in Braille for congenitally blind participants. Participants also completed a timed auditory subtraction task to assess basic mathematical abilities. Finally, participants completed an auditory approximate number discrimination task to assess numerical approximation abilities. On each trial of the approximate number discrimination task, participants judged which of two tone sequences was more numerous. Measures were taken to prevent participants from counting and relying on non-numerical features. Crucially, the ratio between the quantity of tones in the two sequences varied from hardest to discriminate (ratio 1.08, e.g. 16 vs. 15 tones) to easiest to discriminate (ratio 2, e.g. 16 vs. 8 tones). I fit a psychophysical model to each participant's accuracy scores. The only free parameter of this model is the Weber fraction, which indexes the precision of participants' underlying approximate number representations (Odic, Libertus, Feigenson, & Halberda, 2013). Unlike measures of overall accuracy used in previous work, psychophysics enables us to more accurately capture the pattern of performance on this task and understand the precision of underlying number representations.

I found a striking similarity between blind and sighted participants' performance on the timed subtraction task and precision of approximate number representations (Figure 1). Furthermore, I found that individual differences in numerical approximation abilities were correlated with math performance. Together, these methods show that representations of approximate number that are relevant to mathematical thinking develop typically despite the absence of rich numerical information present in visual input. The building blocks of numerical thinking, as measured by behavior, develop independently of visual experience.

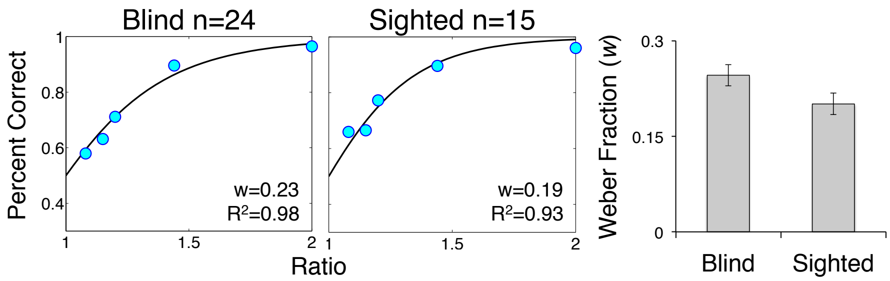

Figure 1. Performance on approximate number discrimination task. Two left graphs show average percent correct for each ratio (blue dots). Black line shows best fitting psychophysical function and corresponding Weber fraction (w) shown in corner. Right graph shows average Weber fraction across subjects in each group. Error bars represent standard error of the mean (SEM).

Chapter 3: Preservation and change in the neural basis of symbolic number processing in blindness

Published as Kanjlia, Lane, Feigenson, & Bedny (2016), Proceedings of the National Academy of Sciences

Although the behavioral signatures of basic numerical abilities are preserved in the absence of vision, it remains possible that these abilities depend on different neural mechanisms. In typically developing sighted individuals, regions of the intraparietal sulcus (IPS) are active during numerical approximation by as early as 4-years of age and spatial patterns of activity in the IPS code for specific numerosities (Cantlon, Brannon, Carter, & Pelphrey, 2006; Eger et al., 2009). In addition to numerical approximation, the IPS is active during mathematical calculation and responds to mathematical statements across a wide range of math subjects (Amalric & Dehaene, 2016; Menon, Rivera, White, Glover, & Reiss, 2000). As stated above, it is possible that representations of number are established in the IPS as a result of numerical information carried by upstream visual input. If so, responses to number, both approximate quantities and exact mathematical processing, would be affected in individuals who have never had any visual experience.

I used task-based fMRI to ask how the neural basis of numerical thinking is modified by atypical visual experience. I asked whether, in congenitally blind individuals, the IPS is recruited to a greater degree during mathematical calculation than during a control sentence comprehension task. Seventeen congenitally blind and 19 sighted individuals judged whether the value of an unknown variable was identical across two spoken math equations (e.g. 7-2=x, 5-3=x). To control for the working memory demands of this equivalence task, I designed a closely matched sentence comprehension task in which participants decided if the meaning of pairs of spoken sentences was the same.

I used region-of-interest (ROI) analysis to further probe whether the IPS was sensitive to the difficulty of math equations in both congenitally blind and sighted groups. I manipulated the difficulty of math equations along two orthogonal dimensions—half of the trials consisted of math equations with single-digit numbers and half with double-digit numbers. Orthogonally, half of the trials were algebraically simple (e.g. 7-2=x) and half were algebraically complex (e.g. x-2=7).

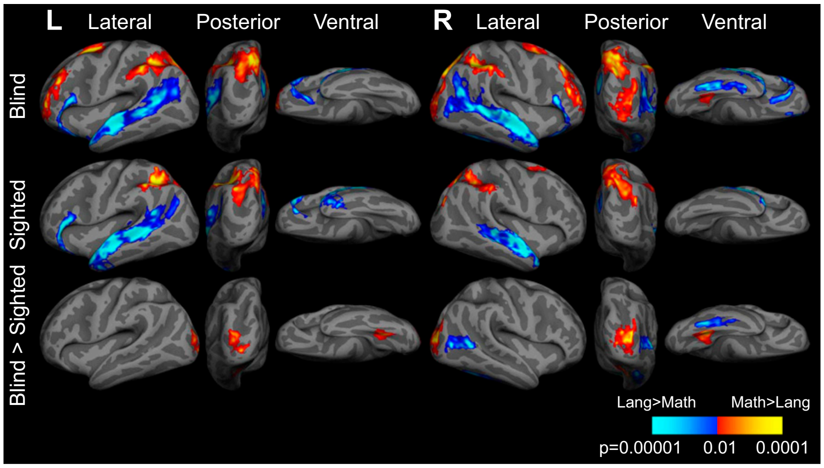

Figure 2. Whole-cortex responses to math and language tasks. Group-level whole-cortex responses to math (warm colors) and language (cool colors) ($p<0.05$, cluster-corrected; $p<0.01$ voxel-wise threshold).

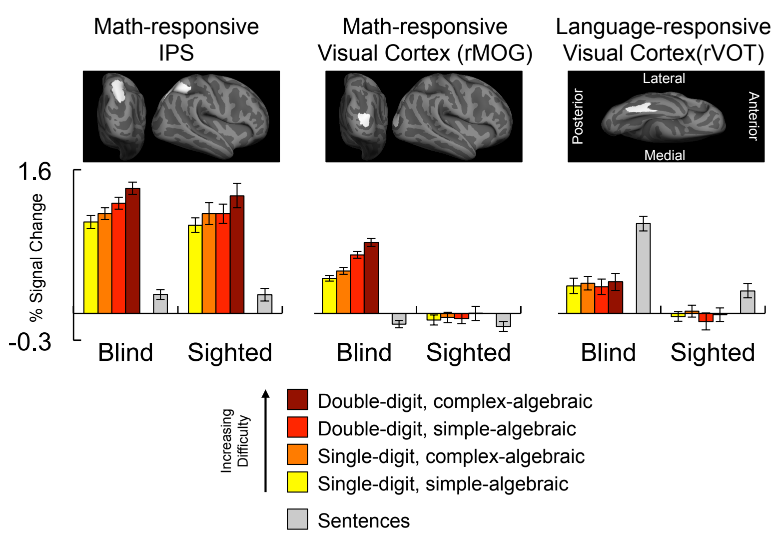

Figure 3. Region-of-interest (ROI) analysis. Responses to each of the four math conditions (warm colors) and sentence condition (gray) in IPS (left), math-responsive 'visual' cortex (middle), and language-responsive 'visual' cortex (right) ROIs. Error bars represent SEM.

In whole-cortex and ROI analyses, I found that the IPS responded more during math calculation than sentence comprehension and ROI analyses revealed that the IPS was sensitive to the difficulty of math equations in both congenitally blind and sighted groups (Figures 2 & 3).

These data show, for the first time, that responses to math in the IPS develop independent of visual experience.

Although the canonical neural responses to number were preserved in blind individuals, we found that blindness modified the neural basis of numerical thinking in a surprising way. In blind but not sighted individuals, parts of dorsal occipital cortex responded to math in a manner similar to the IPS. I also observed responses to sentences in lateral occipital cortices of blind individuals, replicating previous findings (Kim, Kanjlia, Merabet, & Bedny, 2017; Lane, Kanjlia, Omaki, & Bedny, 2015). We hypothesize that 'visual' cortex responses to math and language may be instances of a broader pattern whereby parts of the 'visual' cortex are incorporated into higher cognitive networks (Bedny, 2017). Under this framework, in the absence of bottom-up visual input, 'visual' cortices are "taken-over" by higher cognitive networks with which they are anatomically and functionally connected. In the next chapter, I test this prediction directly using analyses of functional connectivity between math- and language-responsive 'visual' cortices and canonical math and language networks.

Chapter 4: Region-specific increases in fronto-occipital resting-state synchrony mirror functional sub-specialization of visual cortex for higher cognitive functions

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I employed a different method of fMRI analysis, resting-state functional connectivity analysis, to investigate the potential mechanisms underlying plasticity for higher cognitive functions in the 'visual' cortex of blind individuals. We hypothesized that connectivity between deafferented 'visual' cortices and higher cognitive math and language networks underlies the patterns of functional reorganization we observe in the 'visual' cortex of blind individuals (Bedny, 2017). If so, regions of the 'visual' cortex that are recruited during mathematical calculation in blind individuals should be coupled with the canonical number network even in the absence of a task (i.e. at rest) while language-responsive 'visual' regions should be coupled with the canonical language network at rest.

I used task-based fMRI data to identify math- and language-responsive 'visual' regions in the blind group and math- and language-responsive prefrontal regions in blind and sighted groups. I collected resting-state fMRI data from a larger pool of 25 congenitally blind and 43 sighted individuals and correlated resting-state activity in math- and language-responsive 'visual' regions with activity in math- and language-responsive prefrontal regions.

Consistent with our hypothesis, I observed a double-dissociation in resting-state functional connectivity patterns between the two 'visual' and two prefrontal regions. In blind individuals, activity in math-responsive 'visual' cortex was more correlated with that of math-responsive prefrontal cortices than that of language-responsive prefrontal cortices, and vice versa for language-responsive 'visual' cortex. These region-specific enhancements in functional connectivity suggest that parts of deafferented 'visual' cortex are incorporated into distinct higher cognitive networks in the absence of vision.

Interestingly, the dissociation in functional connectivity between math- and language-responsive 'visual' cortices and math- and language-responsive prefrontal cortices was present to a smaller degree even in the sighted group, in whom the visual cortex responded neither to math nor language. This finding raises the interesting possibility that there are pre-existing biases in functional connectivity between different regions in the visual cortex and higher cognitive networks. These biases may be shared across blind and sighted individuals alike and may be enhanced in the absence of bottom-up visual input. Enhanced coupling with specific higher cognitive networks may underlie the functional reorganization we observe in the 'visual' cortex of congenitally blind individuals. Thus, the combination of resting-state and task-based fMRI analyses in congenitally blind individuals has provided new insights regarding potential mechanisms underlying 'visual' cortex reorganization.

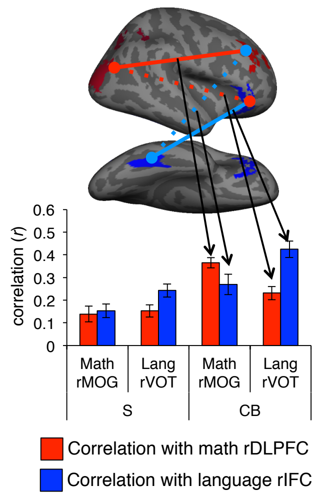

Figure 4. Resting-state functional connectivity between math- and language-responsive 'visual' and prefrontal cortices. Correlations between activity in 1) math-responsive visual cortex (rMOG), 2) language-responsive 'visual' cortex (rVOT), 3) math-responsive prefrontal cortex (rDLPFC), and 4) language-responsive prefrontal cortex (rIFC). Functional connectivity in sighted group (S) on left and blind group (CB) on right. Error bars represent SEM.

Chapter 5: Repurposing of visual cortex for number is restricted to sensitive periods in development

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An integral factor in the debate on the role of nature versus nurture in development is timing. Whereas the capacity of nurture to shape development is greater early in life, the capacity of the mind and brain to undergo experience-dependent changes tends to narrow over development. Therefore, a key question in the fields of cognitive and neural development and neuroplasticity concerns sensitive periods in development. In Chapter 5, I asked whether the plasticity observed in the 'visual' cortex of congenitally blind individuals is restricted to sensitive periods in development or can even occur following total blindness later in life. I compared patterns of plasticity in the 'visual' cortex across individuals who are blind from birth, those who become blind in adulthood (after the age of 17) and sighted individuals.

Thirteen adult-onset blind, 20 congenitally blind and 19 sighted individuals completed the math and language fMRI task described in Chapter 3. In whole-cortex analyses, I found that 'visual' cortex responses to math and language were present exclusively in congenitally blind individuals and not individuals who became totally blind in adulthood (Figure 5). Region-of-interest analyses reveal that the 'visual' cortex of adult-onset blind individuals was not sensitive to math difficulty (Figure 6).

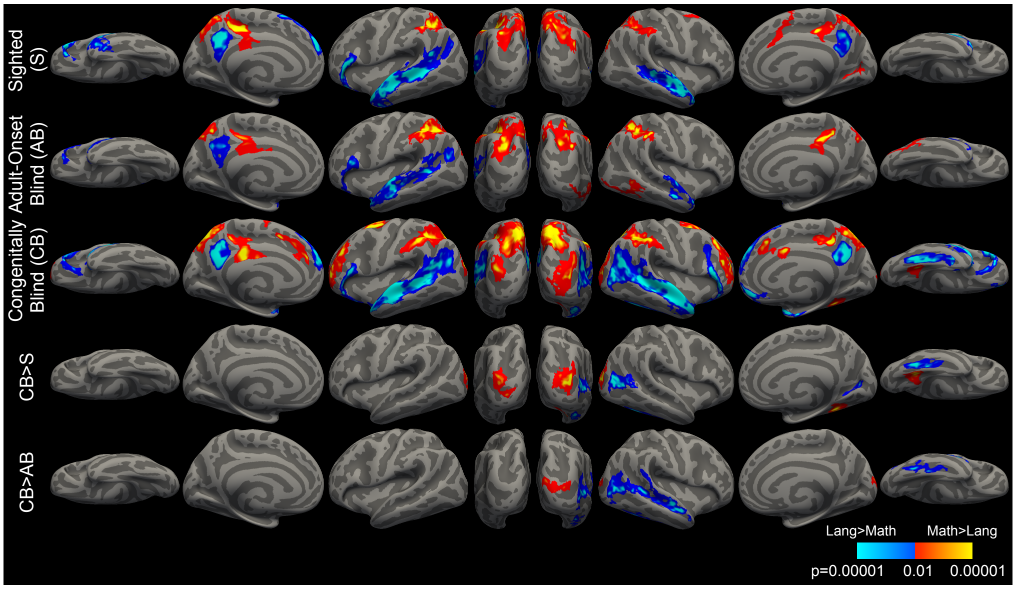

Figure 5. Whole-cortex responses to math and language. Responses to math (warm colors) and sentences (cool colors) ($p<0.05$, cluster-corrected; $p<0.01$ voxel-wise threshold).

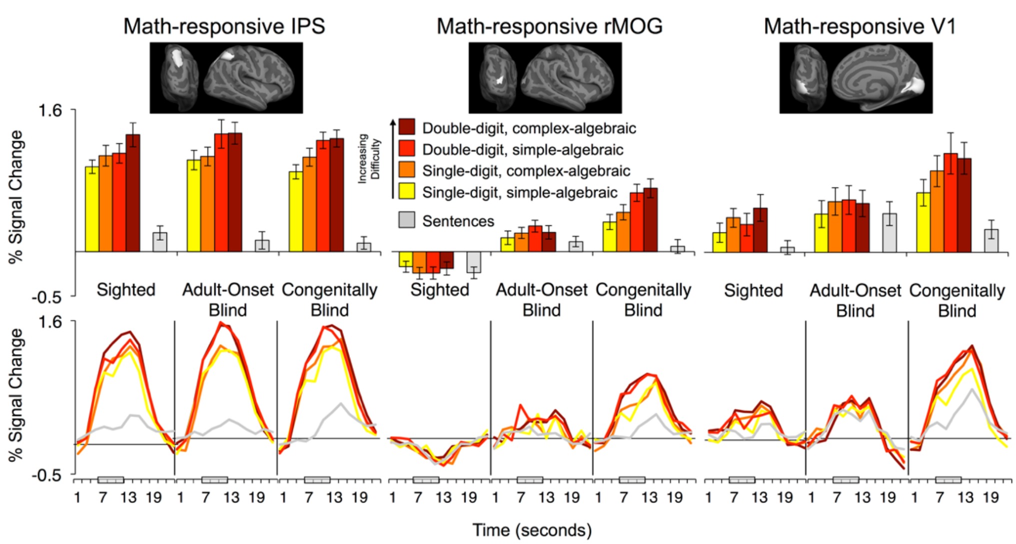

Figure 6. Region-of-interest analyses. Percent signal change relative to rest for each of the four math conditions (warm colors) and sentence condition (gray). Time-course of activity in each region shown in bottom panel, percent signal change averaged over peak window (shown with gray bar on x-axis) in top panel.

In Chapter 4, I observed that 'visual' cortex recruitment for math and language in the congenitally blind group was related to increased functional connectivity with canonical higher cognitive networks. I therefore asked whether the absence of math and language responses in the 'visual' cortex of adult-onset blind individuals could be explained by reduced coupling with higher cognitive networks. Surprisingly, I found that regions of the 'visual' cortex that respond to math and language in congenitally blind individuals show *increased* functional connectivity with math- and language-responsive prefrontal regions, respectively, in adult-onset blind individuals (Figure 7).

Note that these region-specific enhancements in resting-state functional connectivity occur despite the absence of task-based math and language responses in the 'visual' cortex of adult-onset blind individuals. Together, these findings suggest that, in blindness, sensitive periods do not preclude enhanced coupling between 'visual' cortices and higher cognitive networks. However, this increased functional connectivity is not sufficient for 'visual' cortex plasticity. It is when interactions between 'visual' and higher cognitive cortices are established early in development that responses to higher cognitive functions are observed in the 'visual' cortex. The combination of resting-state and task-based analyses have, therefore, begun to elucidate potential mechanisms by which sensitive periods operate in plasticity following sensory loss.

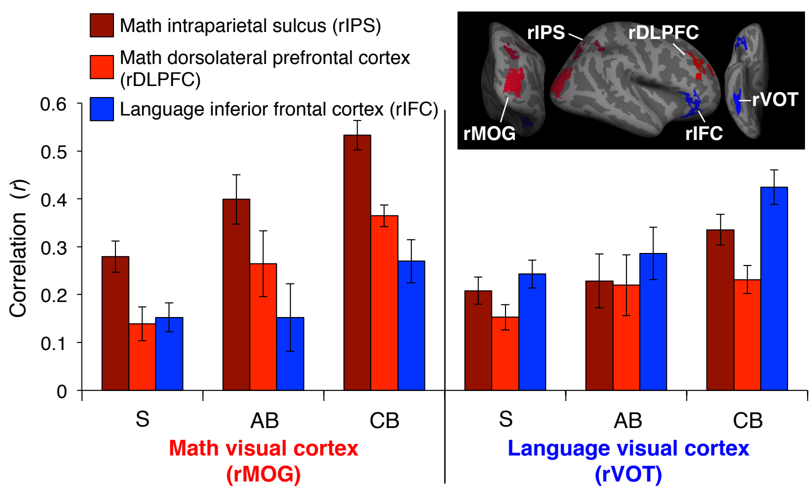

Figure 7. Resting-state functional connectivity between math- and language-responsive 'visual' cortices and math- and language-responsive prefrontal and parietal cortices. Correlation between activity in math- (left) and language-responsive 'visual' cortex (right) and fronto-parietal regions of interest in sighted (S), adult-onset blind (AB) and congenitally blind (CB) groups.

Chapter 6: The neural basis of approximate number in congenital blindness

In preparation as Kanjlia, Feigenson, & Bedny, bioRxiv 573436.

Thus far, I have used a combination of cognitive testing, psychophysics, tasked-based fMRI and resting-state fMRI to demonstrate that the cognitive and neural basis of numerical thinking is largely preserved in the face of drastically different sensory experience. However, this preservation is accompanied by plasticity in deafferented 'visual' cortices in congenital blindness.

A key outstanding question that remains to be tested directly is whether the IPS develops representations of non-symbolic, approximate quantities in the absence of visual experience. Are representations of approximate quantities localized to the same cortical regions in sighted individuals, who can experience hundreds of items in less than a second in vision, and congenitally blind individuals who have only ever experienced quantities through sound and touch?

To answer this question, it was necessary to define a neural measure that would capture more fine-grained differences in cognitive representations of approximate number (i.e. a neural measure that would differentiate between the cognitive representation of 4 vs. 8 items). Multivariate pattern analysis (MVPA) of fMRI data has been able to provide a closer look at the cognitive representations coded in cortical regions (Norman, Polyn, Detre, & Haxby, 2006). I, therefore, leveraged MVPA to test whether quantities are actually coded in spatial patterns of activity in the IPS (Eger et al., 2009).

I presented 16 congenitally blind and 18 sighted participants with sequences of 4, 8, 16 or 32 beeps. For every numerosity pair, I trained a machine-learning classifier with the patterns of IPS activity associated with the two numerosities (e.g. 8 and 16 beeps) and then tested the classifier's ability to identify the numerosity associated with left-out (unlabeled) IPS activity patterns. In addition to this region-of-interest-based approach, I conducted this analysis in searchlights across the entire cortex.

Recall that, in behavior, quantities that differ by larger ratios (e.g. 4 vs. 32) are easier to discriminate than those that differ by smaller ratios (e.g. 4 vs. 8). This signature is thought to reflect greater representational overlap between quantities that differ by smaller ratios. (Feigenson et al., 2004; Gallistel & Gelman, 2000). This cognitive model makes specific predictions regarding the discriminability of IPS activity patterns associated with numerosities that differ by smaller versus larger ratios. As the ratio between quantities increases, our machine-learning classifier should become more accurate at discriminating their corresponding neural patterns.

Auditory quantities were discriminable in the IPS of both congenitally blind and sighted individuals based on both ROI and searchlight analyses (Figures 8 & 9). Furthermore, quantities that differed by smaller ratios were less neurally discriminable than those that differed by larger ratios. Together with results from Chapters 2 and 3, these findings demonstrate that the cognitive and neural signatures of numerical thinking are not compromised by drastically different histories of visual experience.

Furthermore, approximate quantities were reliably discriminable in regions of the 'visual' cortex that were recruited during mathematical calculation in congenitally blind individuals (Chapter 3). Although quantity discrimination was successful in the math-responsive 'visual' region in both blind and sighted individuals, the ratio-dependent signature of numerical approximation was only observed in the 'visual' cortex of the congenitally blind group. The MVPA approach used in this study, therefore, expand on our findings from Chapter 3 by showing that, in addition to demonstrating univariate responses to math difficulty, math-responsive 'visual' regions may actually develop a more fine-grained code for numerosity in congenital blindness.

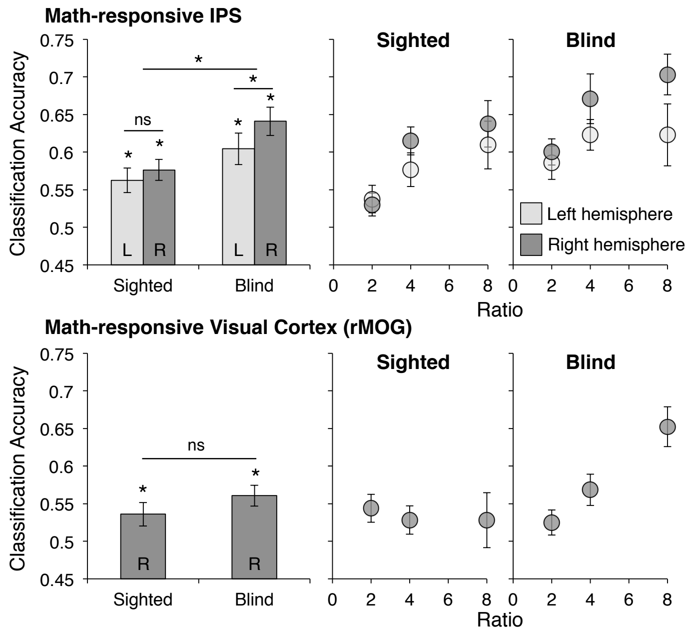

Figure 8. MVPA Classification accuracy. Classifier accuracy for discriminating neural patterns of activity associated with numerosities. Bar graphs on left show classification accuracy averaged across all pairwise numerosity comparisons. Scatter plots on right show classification accuracy for each ratio category.

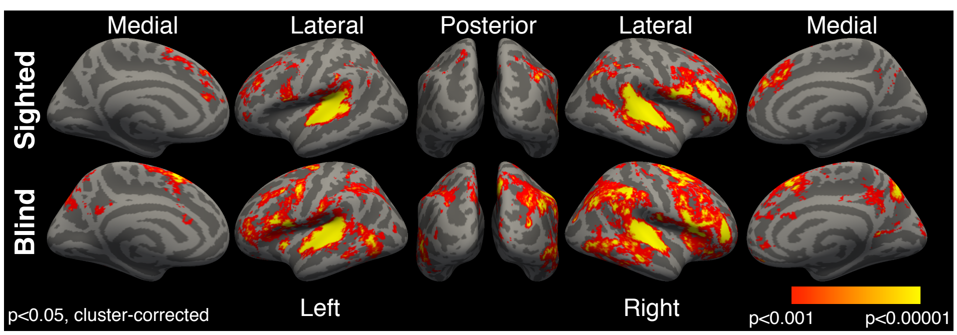

Figure 9. Searchlight MVPA. MVPA conducted in searchlights with 10mm radius across entire cortex (p<0.05, cluster-corrected; p<0.01 voxel-wise threshold).

Chapter 7: Discussion and conclusions

Understanding the ways in which experience shapes the mind and brain has far-reaching implications--for educators who are working with the minds of the next generation to neurologists aiding patients suffering from stroke. The goal of this dissertation was to form a deeper understanding of how a case of drastically different life experience modifies the cognitive and neural basis of an important cognitive domain. Numerical cognition, development, plasticity, the visual cortex and blindness have been studied extensively in separate research programs. Integrating these areas of research provided an opportunity to break new ground on the age-old philosophical, psychological and neurological question of the role of nature and nurture in development.

My research program investigated the role of visual experience in the cognitive and neural development of one the most important human cognitive faculties—numerical thinking. I worked with congenitally blind individuals, who have never seen sets of objects, to show that many of the cognitive and neural signatures of non-symbolic and symbolic numerical thinking are impervious to the absence of vision.

The precision of approximate number representations, as measured by psychophysics, is not compromised in congenitally blind individuals and is correlated with fundamental mathematical abilities (Kanjlia, Feigenson, & Bedny, 2018; Chapter 2). Furthermore, IPS representations of approximate number and involvement in mathematical calculation, as measured by fMRI, is remarkably similar across congenitally blind and sighted individuals (Kanjlia, Lane, Feigenson, & Bedny, 2016; Kanjlia, Feigenson & Bedny, In Prep; Chapter 3 & 6). By leveraging tools in cognitive science and neuroimaging, this work provides compelling evidence for the resilience of numerical thinking and its neural basis in the face of atypical sensory experience.

Experience did, however, play a significant role in the plasticity of deafferented 'visual' cortices in congenital blindness. Using task-based fMRI, I show that, in congenitally blind but not sighted individuals, parts of the 'visual' cortex were recruited during math calculation and were distinct from 'visual' cortices that were active during sentence processing (Kanjlia et al., 2016; Chapter 3). Multivariate pattern analysis revealed that this math-responsive 'visual' region even codes for approximate quantities in a ratio-dependent manner in congenitally blind individuals (Kanjlia et al., In Prep.; Chapter 6). To explore potential mechanisms underlying this math-related plasticity, I employed resting-state fMRI analyses and showed that regional specialization of the 'visual' cortex for math and language is related to connectivity with canonical math and language networks (Kanjlia et al., 2016; Chapter 4). Finally, I worked with an additional population of adult-onset blind individuals to demonstrate that the capacity for dramatic 'visual' cortex plasticity narrows over development (Kanjlia, Pant, & Bedny, 2018; Chapter 5).

The preservation of the IPS number system in congenital blindness suggests that early number representations do not require experience to be established or can be formed after experience in any sensory modality. By contrast, functions of the visual cortex are strongly tied to the visual modality. Therefore, in the complete absence of visual input, visual cortex functions are compelled to undergo more dramatic functional changes, potentially driven by top-down input from higher cognitive networks. By integrating conceptual and technical advances from several disciplines, this work has revealed the harmonious interplay between preservation and plasticity, nature and nurture, in the domain of numerical thinking.

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