Built to adapt: mechanisms of cognitive flexibility in human brain.

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Abstract

Adaptability is a distinguishing feature of the human species: we thrive as hunter-gatherers, farmers, and urbanites. What properties of our brains make us highly adaptable? We review neuroscience studies of sensory loss, language acquisition, and cultural skills (reading, mathematics, programming). The evidence supports a 'flexible specialization' account. On the one hand, adaptation is enabled by evolutionarily prepared flexible learning systems, both domain-specific social learning systems (e.g., language) and domain-general systems (fronto-parietal reasoning). On the other hand, the functional flexibility of our neural wetware enables us to acquire cognitive capacities not selected for by evolution. Heightened plasticity during a protracted period of development enhances cognitive flexibility. Early in life, local cortical circuits are capable of acquiring a wide range of cognitive capacities. Exuberant cross-network connectivity makes it possible to combine 'old neural parts' in 'new ways,' enabling cognitive flexibility such as language acquisition across modalities (spoken, signed, braille) and cultural skills (math, programming). Together, these features of the human brain make it uniquely adaptable.

1. Introduction

Anthropologists have long pointed out that humans occupy a wide range of habitats and exhibit diverse knowledge and behavior (e.g., Mead, 1928; Benedict, 1935; Boas, 1896; Tooby & DeVore, 1987; Henrich & McElreath, 2003). We thrive as hunter gatherers in the Kalahari Desert and the Arctic, as computer programmers in Taipei, and as potato farmers in Idaho. Most humans today live in environments far different from those for which our brains were evolutionarily 'optimized.' Human cognitive diversity is also evident within a given location and time period. Many societies are characterized by a division of labor: some of us grow food, become experts in medicine, or teach children, while others design housing, fly airplanes, or program computers (Durkheim, 1947; Lutz & Keil, 2002). Humans likewise thrive across different sensory experiences, such as deafness and blindness (e.g., Landau & Gleitman, 1985; Padden & Humphries, 2006). Our ability to adapt to varied experiences, both across and within societies, is distinctive in the animal kingdom and paramount to our survival (Boyd et al., 2011; Tooby & DeVore, 1987; Tomasello, 1999; Tooby & Cosmides, 1992; Legare, 2017). Here we discuss the neural mechanisms that enable this unparalleled adaptability.

Drawing upon psychological and cognitive neuroscience studies of variation in human experience, we propose a 'flexible specialization' account. Our unusual adaptability is supported by a combination of i) evolutionarily prepared neural systems that enable distinctively human flexible learning and ii) the functional plasticity of the human brain and its consequent ability to support cognitive capacities not selected for by evolution.

Human brains have a distinctive evolutionarily prepared capacity for flexible learning. Specific neural mechanisms are predisposed to develop into domain-specific and domain-general flexible learning systems. Language is an example of a distinctively human 'domain-specific' system that enables flexible learning through social communication. Domain-general reasoning systems in fronto-parietal cortices are likewise elaborated in humans and evolutionarily prepared to support novel problem solving and learning (Duncan, 2010; Woolgar et al., 2016; Badre & Nee, 2018). These are examples of specific adaptation for flexible learning.

On the other hand, human adaptability is made possible by the functional flexibility of neural wetware. Our brains are built to go beyond built-in cognitive capacities through functional plasticity. As David Marr observed, mental 'software' is partly independent from the hardware in which it is implemented (Marr, 1982). Neural structures have a range of 'cognitive affordances,' including affordances for cognitive functions that bear no resemblance to the 'software' for which they originally evolved. Several properties of the human brain contribute to its flexibility. Local cortical circuits are *cognitively pluripotent*, capable of supporting a range of cognitive operations. Exuberant cross-system connectivity makes it possible to combine 'old neural parts' in 'new ways' not selected for by evolution. Finally, increased plasticity during protracted human development enhances the functional range of local cortical circuits and their connectivity with each other. Together, these properties of the human brain enable us to go beyond what evolution 'intended.'

Studies of variation in experience are key to understanding adaptation. Most humans share a highly similar genetic code as well as many common experiences that shape brain development, such as seeing faces, experiencing gravity, participating in social interactions, and acquiring a natural language. Where people share both genetics and experience, we cannot tease apart their respective contributions to neural function and behavior. Comparing brain function across subsets of the population for whom experience differs in systematic ways (e.g., blindness, literacy, programming expertise) offers insight into the causal mechanisms of neural specialization and flexibility.

The current article integrates evidence from neuroscience studies of sensory loss (i.e., blindness) as well as linguistic and cultural variation. These examples of variation in human experience are often separated in the literature. Blindness is the absence of a 'species-typical' sensory experience, whereas cultural learning is the 'addition' of socially constructed skills (Greenough et al., 1987). At the same time, all of these forms of adaptation are subject to common biological constraints. Some of the same uniquely human cognitive mechanisms that enable the acquisition of socially constructed cultural skills also enable adaptation to sensory loss.

People who are born blind use social learning and linguistic communication to construct causal models of visual phenomena (e.g., color, seeing) (Landau & Gleitman, 1985; Kim et al., 2019; Campbell & Bergelson, 2022). Blind people invent and use adaptive tools such as canes for navigation, tactile braille symbols for reading, and screen readers for searching the internet. Deaf infants learn the sign language of their community, and if not exposed to an accessible visual-manual language, begin to create one (Goldin-Meadow, 2005; Carrigan & Coppola, 2017; Kocab et al., 2016). Deafness has given rise to a rich culture, replete with stories, social customs, and traditions (Padden & Humphries, 2006). Blindness and d/Deafness are therefore not merely a loss in sensory access, but also a gain of identity, community, skills, and culture (Barnes, 2016). This remarkable capacity to adapt and thrive in sensory loss is quintessentially human. Bringing together evidence from studies of sensory loss and cultural variation provides a more complete understanding of the mechanisms that make human adaptation possible.

1.2 The relationship of the current account to previous proposals

One proposal from which we draw inspiration is Dehaene & Cohen's (2007) cultural recycling of cortical maps. The current account shares with that proposal the idea that modification of innate domain-specific circuitry is an important mechanism of cultural adaptation. We do not discuss this mechanism in detail in the current article mainly because it is laid out clearly in Dehaene & Cohen (2007). However, in our view, the subtle modification of innate domain-specific maps is insufficient to explain the breadth of human behavioral adaptation as well as evidence for functional plasticity in human cortex. Moreover, many of the domain-specific systems that have been identified in humans are shared across species (Carey, 2009; Spelke, 2022), yet humans stand out in their adaptability. In the current account, we highlight uniquely human learning mechanisms (e.g., language) that enable the distinctively wide range of human behavior. We also propose a more extensive capacity for instantiating new cognitive content in anatomical circuits during development. Finally, we emphasize the role of exuberant connectivity between neural systems and the contribution of domain-general reasoning circuits to human adaptability. In short, we suggest that human cortex is more open-endedly flexible than the original cultural recycling account suggests.

In highlighting the role of flexible learning, our account shares some features with proposals that emphasize domain-general learning mechanisms (e.g., Quartz & Sejnowski, 1997; Heyes, 2018). For example, the 'cognitive gadgets' account proposes that associative learning processes give rise to neural gadgets that support varied human cognitive abilities, from reading to social cognition to language (Heyes, 2018). We agree that experience, including cultural experience, enables the human brain to acquire software that has not been 'hard-coded' into neural circuits. However, a variety of evidence, some of which we discuss below, suggests that human brains are evolutionarily prepared for language and social cognition in ways that are different from cultural inventions such as reading. Unlike proposals that rely on domain-general learning alone, the flexible specialization account emphasizes the contribution of evolutionarily prepared, domain-specific neurocognitive systems to human cognition and adaptability.

In arguing that the same neural wetware can implement different cognitive software, our account is related to the neural reuse proposal (Anderson, 2010). We agree with Anderson (2010) that the loose relationship between structure and function makes human brains adaptable and computationally powerful. However, in our account this adaptability comes in the form of functional potential at birth and variation across the population rather than a lack of specialization within individual brains. The reuse account proposes that the same neural tissue supports varied cognitive tasks within an individual from moment to moment, such that there is no specialization of neural systems for specific cognitive content. In particular, 'high-level' and evolutionarily recent 'tasks' such as language and social cognition are not associated with specific neural substrates. Cortical circuits instead have built-in abstract computations or 'workings' which apply across cognitive domains (Anderson, 2010). Contrary to this idea, there is evidence that within individuals, neural systems show high specialization for linguistic communication (Fedorenko et al., 2011) and social cognition (Saxe & Kanwisher, 2003) as well as for perceptual functions, such as face, body, and action perception (Kanwisher et al., 1997; Isik et al., 2017). At the same time, the recruitment of visual cortices for low-level perception in sighted people and for language, executive control, and mathematics in people born blind suggests that neural wetware can acquire different software as a function of experience, i.e., there are no immutable cognitive 'workings.' Cognitive flexibility and specialization of cortical circuits coexist.

The remainder of the paper is organized as follows. First, we describe five proposed mechanisms of adaptation (Figure 1, Section 2). The first two mechanisms are evolutionarily prepared neurocognitive systems that enable uniquely human flexible learning: language is an example of a domain-specific social learning mechanism (2.1) and fronto-parietal reasoning circuits are an example of a domain-general mechanism (2.2). The last three mechanisms are properties of the human brain that enable functional plasticity: heightened plasticity during development (2.3), cognitive pluripotency of cortical circuits (2.4), and exuberant cross-system connectivity (2.5). Next, we review empirical examples of adaptation that provide evidence for these mechanisms (Section 3): blindness (3.1), language acquisition (3.2), and acquisition of cultural symbol systems (reading, math, and programming) (3.3). All of these examples of adaptation make use of all the proposed mechanisms, but to different degrees. We end by summarizing our proposal and discussing open questions and future directions.

2. Mechanisms of adaptation in the human brain: An overview

2.1 Evolutionarily prepared social learning systems: the case of language

Human brains are prepared for social learning (e.g., Saxe, 2006; Tomasello, 1999; Wellman et al., 1990; Gopnik & Wellman, 1992; Spelke, 2022; Carey, 2009; Gweon, 2021). Our ability and desire to learn from others allows us to adapt to varying physical and cultural environments as well as to sensory loss. Social learning also enables 'cultural ratcheting,' or the improvement of technology, skills, and knowledge over generations (Tomasello, 1999; Tennie et al., 2009). The highly complex phenomenon of social learning depends on multiple distinct neurocognitive systems, each with a different neurobiological substrate, including the so-called 'mentalizing' system, which supports our understanding of the minds and actions of others (Woodward, 1998; Saxe & Kanwisher, 2003; Gopnik & Wellman, 1992). Human social learning also critically depends on language, which enables efficient communication (Pinker, 2010; Tooby & DeVore, 1987; Lupyan et al., 2007; Gelman, 2009). In this paper, we treat language as a case study of a domain-specific neurocognitive system that evolved to enable adaptability through social learning.

As discussed in more detail below, language processing is likely supported by an evolutionarily prepared neurobiological system that, in its mature state, is domain-specific and relatively modular (i.e., operates over a restricted class of representations) (e.g., Chomsky, 1965; Broca, 1861; Bellugi, et al., 1989; Fedorenko & Varley, 2016). However, the neural and communicative/informational flexibility of the language system is key to its adaptive utility.

The cognitive pluripotency of the neural network that supports language and its heightened flexibility during development enables the acquisition of varied languages. Exuberant connectivity between the language network and other neural systems enables language processing in any modality: auditory, visual-manual, and tactile. Efficient communication with other neural networks also enables the recruitment of the language system for cultural technologies, including reading, math, and programming (Dehaene et al., 2002; Price et al., 1996; Friedrich & Friederici, 2013; Maruyama et al., 2012; Liu et al., 2024).

Language is also flexible in the information that it delivers. As recent large language models (LLMs) aptly demonstrate, almost anything can be learned through linguistic communication (e.g., Petroni et al., 2019). This feature of language makes it a powerful tool for learning and cultural transmission (Pinker, 2010; Tooby & DeVore, 1987; Gelman, 2009). For example, children use language to learn about mental states, the causes of illnesses, religious beliefs, the life cycle, and moral norms (i.e., Harris & Koenig, 2006; Legare & Gelman, 2008; Spelke, 2022; Gelman, 2009). People born blind construct causal mental models of visual phenomena based in part on information acquired via linguistic communication (Landau & Gleitman, 1985). It is hard to imagine an aspect of human culture where linguistic communication does not play a role.

2.2 Domain-general fronto-parietal reasoning systems

In addition to specialized domain-specific systems, human adaptation depends on evolutionarily prepared domain-general reasoning abilities that are supported by fronto-parietal circuits and prefrontal cortex. Multiple properties of these networks make them well suited to support cultural learning. Unlike domain-specific systems, domain-general networks operate over a wide range of stimuli, from words and faces to colors and cultural symbols like the algebraic variables X and Y (e.g., Duncan, 2010). Exuberant connectivity between these networks and the rest of the brain allows them to integrate information across domains (Sporns, 2022). Domain-general reasoning networks also participate in novel, cognitively demanding executive and working memory tasks (e.g., n-back) (Vendrell et al., 1995; Yaple et al., 2019; Thompson-Schill, 1997).

In human brains, fronto-parietal domain-general circuits support the learning and maintenance of abstract rules and deductive reasoning, which are important for cultural symbol systems like mathematics and programming (Badre et al., 2010; Woolgar et al., 2016; Coetzee & Monti, 2018; Danker & Anderson, 2007). Moreover, in non-human primates, prefrontal neurons encode conditionals such as, if cue A, then respond to a matching stimulus; if cue B then respond to a non-match (Wallis et al., 2001; Hoshi et al., 2000) as well as numerical rules such as 'greater than' vs 'smaller than' (Bongard & Nieder, 2010; Eiselt & Nieder, 2013). Such representations could play a role in logical reasoning tasks.

The large-scale expansion of prefrontal and fronto-parietal networks in humans is thought to enable unique abstract reasoning, planning, and goal-driven behavior in our species (e.g., Badre & Nee, 2018). These domain-general networks also mature later than other parts of the brain, with synaptic pruning and myelination continuing into adolescence (e.g., Gogtay et al., 2004; Huttenlocher & Dabholkar, 1997). The protracted development of human domain-general networks positions them to support later-acquired cultural skills.

2.3 Enhanced plasticity of developing cortical circuits

Enhanced plasticity early in development is found across cortical systems, from vision to language, although the timing of different developmental trajectories differs widely (Hensch, 2018). Protracted neural development in humans likely bolsters our adaptability. Decades of evidence from studies of behavior and brain function suggests that human brains are more flexible early in life (e.g., Lenneberg, 1967; Lewis & Maurer, 2005; Maurer & Werker, 2014; Werker & Hensch, 2015). For example, as discussed in more detail below, congenital sensory loss has much larger effects on the function of sensory cortices compared to acquired sensory loss (e.g., Cohen et al., 1999; Burton, 2003; Sadato et al., 2002; Musz et al., 2022). Studies with animal models have identified a variety of cellular and molecular mechanisms that render neural circuits more functionally flexible during 'critical periods' of development (Hensch, 2004, 2005; Hubel & Wiesel, 1970; Crair et al., 1998). For example, distinctive properties of the excitatory-inhibitory balance in primary visual cortex early in life enhance synaptic malleability and sensitivity to experience (Morishita & Hensch, 2008). The conclusion of critical periods is marked by stabilizing structural changes, such as the formation of perineuronal nets, which also curb synaptic plasticity (Pizzorusso et al., 2002).

Humans undergo protracted neural development compared to other primates, providing a longer opportunity for experience to influence brain function (Sherwood & Gomez-Robles, 2017; Hartley, 2022). Neurodevelopmental processes such as synaptogenesis, synaptic pruning, and myelination unfold throughout childhood, with many higher-cognitive regions reaching full maturity only after adolescence (Huttenlocher, 2009; Gogtay et al., 2004; Larsen & Luna, 2018; Huttenlocher & Dabholkar, 1997; Yeung et al., 2014). The extended neural development of higher-cognitive systems and their expansiveness in the human brain enhances adaptability.

2.4 Cognitive pluripotency of local cortical circuits

Distinct cortical areas are characterized by layers of different thickness, different distributions of cell types, and different inter-neuronal connectivity patterns (Passingham et al., 2002; Jorstad et al., 2023). There is also covariation between these cytoarchitectural features and cortical functions (e.g., some visual areas have a characteristic cytoarchitecture e.g., Amunts & Zilles, 2015; Weiner et al., 2017). These observations could suggest that anatomy dictates function (e.g., Makin & Krakauer, 2023). Contrary to this idea, studies of sensory loss suggest that the same cortical tissue can represent different cognitive content across individuals as a function of different early life experience (e.g., Kahn & Krubitzer, 2002; Collignon et al., 2009; Bedny, 2017). Local circuits have capacity to encode information for which they were not specifically prepared by evolution (Musz et al., 2023; Von Melchner et al, 2000).

Adaptation in sensory loss provides a particularly striking illustration of this phenomenon (for recent review see Saccone et al., 2024). Cortical circuits thought to have evolved for low-level vision (e.g., V1/BA17) participate in non-visual functions in blindness (e.g., language) (Sadato et al., 1996; Röder et al., 2002; Bedny et al., 2011). This finding suggests that while anatomical properties of local circuits make some computations more efficient than others, these circuits nevertheless have broad computational potential. Cortical circuits are both evolutionarily prepared to develop adaptive functions and functionally flexible. The loose relationship between software and wetware in the human brain is key to adaptation.

Cognitive pluripotency of cortical tissue contributes to all forms of learning, but the degree of functional plasticity varies widely across examples (see Section 2.3). Repurposing of 'visual' cortex for language in blindness is a particularly dramatic example of pluripotency that results in vastly different cortical function in occipital cortex of blind and sighted people. Plasticity within fronto-temporal language networks of children acquiring different languages is an example of more subtle functional plasticity (MacSweeney et al., 2008a; Emmorey, 2021; Malik-Moraleda et al., 2022; Werker & Hensch, 2015). Later acquired cultural skills, such as reading, math, and programming, also depend on the modification of informational content in local cortical circuits, but likely to a lesser degree (Dehaene & Cohen, 2007). In the current review, we operationalize the neuroplasticity that accompanies cultural learning in late childhood and adulthood as the lower end of the cognitive pluripotency 'continuum' (Figure 2).

2.5 Repurposing of exuberant cross-network connectivity

Human cortical systems are densely interconnected, and the reuse of this exuberant cross-network connectivity plays a central role in human adaptability. The brain is comprised of hierarchically organized neural 'networks,' some of which have relatively coherent cognitive functions (e.g., facial perception network, language network; Kanwisher et al., 1997; Fedorenko et al., 2011). While regions within a network are more strongly connected to each other than to other networks, robust cross-network connectivity is a defining feature of human brains (Schaefer et al., 2018; Friederici, 2009; Petersen & Sporns, 2015; Park & Friston, 2013). Cross-network connectivity is particularly pronounced among higher-cognitive circuits (e.g., 'rich club' hubs) and between higher-cognitive and sensory systems (van den Heuvel & Sporns, 2011; Bullmore & Sporns, 2012). There are comparatively fewer direct connections between early sensory areas in the human brain (Qin & Yu, 2013). These features of the human connectome enable adaptability and also shape the particular ways in which we adapt.

Every case of behavioral adaptation discussed in the current article makes use of cross-network connectivity. For example, visual areas take on non-visual functions via connectivity between the visual system and non-visual networks in blindness. Our capacity to acquire and process spoken, visual-manual (sign), and tactile language (braille) depends on connectivity between the language system and sensory cortices. Math and programming likewise depend on connectivity between higher-cognitive and sensory networks, as well as between language and other higher-cognitive neural networks.

The exuberant between-network connectivity of the human brain makes many behaviors possible that were not directly selected for by evolution. The cognitive function supported by a cross-system connection in a given case of adaptation may be related to the function for which the connection originally evolved or may be entirely different. For example, the same anatomical connection that supports top-down attention and prediction during visual perception in sighted people enables 'visual' circuits to participate in executive processes and language in blindness (Striem-Amit et al., 2015; Burton et al., 2014; Deen et al., 2015; Tian et al., 2024). Visual reading depends on connectivity between visual object recognition and language networks, but the evolutionary origins of this connection are unknown (Saygin et al., 2016; Bouhali et al., 2014). How a connection is reused is determined by what we refer to as its 'cognitive affordance,' i.e., the information transfer that it can support given its anatomical location, as well as the behavioral needs of the individual.

3. Examples of neural adaptation: Sensory loss, language acquisition and cultural symbol systems

3.1 Blindness: Adaptation to sensory loss

Blindness offers a key example of how specialization and flexibility coexist in the human brain. The human brain is adapted for visual perception. Sighted people rely on vision for behaviors such as recognition of conspecifics, social communication, and navigation (Kanwisher & Yovel, 2006; Senju & Csibra, 2006; Epstein et al., 2007). Many visual functions are associated with specialized modality-specific neural circuitry (e.g., fusiform face area, parahippocampal place area). A larger portion of the human brain is devoted to vision than any other sensory system (Grill-Spector & Malach, 2004). Many 'visual' neural structures are evolutionarily ancient, i.e., shared across most mammals (Krubitzer, 1995; Espinosa & Stryker, 2012). The human brain is therefore 'built to see.'

Nevertheless, humans who are born blind carry out seemingly visual tasks using non-visual information. Blind and sighted children develop spatial representations, language, social cognition in a remarkably similar manner (e.g., Landau & Gleitman, 1985; Campbell et al., 2024). Blind individuals adapt to sensory loss in uniquely human ways. People who are blind invent, teach, and use non-visual cultural tools, such as braille, canes, guide animals, and text-to-speech software. Blind individuals rely on linguistic communication to acquire rich visual semantic knowledge, including understanding of color, light, and visual perception (e.g., Shepard & Cooper, 1992; Bedny et al., 2019). Neural structures that enable vision in sighted people are repurposed for non-visual functions in blindness, including uniquely human functions like language and cultural inventions like braille reading and mathematics (e.g., Sadato et al, 1996; Röder et al., 2002; Bedny et al., 2011; Kanjlia et al., 2016). Below we review some examples of blindness-related adaptation and discuss what they reveal about the adaptive potential of the human brain.

3.1.1 'Visual knowledge' in blindness

Visual semantics in blindness provides an impressive illustration of flexible social learning via linguistic communication. Concepts such as 'blue,' 'glance,' and 'sparkle' are directly accessible only through the visual modality. British empiricists like Locke and Hume, who emphasized the importance of sensory experience in learning, argued that visual phenomena are inaccessible to blind people (e.g., Locke, 1690; Hume, 1740). Such intuitions persist in modern-day psychology, education, and neuroscience (e.g., Barsalou, 1999; Gallese & Lakoff, 2005; Dunlea, 1989; Bigelow, 1987). The empirical evidence suggests, however, that 'visual' semantic knowledge is qualitatively similar across blind and sighted people. A series of groundbreaking experiments conducted by Landau & Gleitman (1985) showed that congenitally blind children acquire 'visual' words, such as color adjectives and the verbs 'look' and 'see,' around the same time as sighted children (see also Campbell et al., 2024). For example, children born blind understand that physical objects but not ideas have colors. Blind and sighted adults have similar knowledge of color similarity (e.g., blue is more similar to green than to red) and make fine-grained distinctions among acts of visual perception (e.g., stare vs. glance) and light emission events (e.g., sparkle vs. flash) (Shepard & Cooper, 1992; Marmor, 1978; Saysani et al., 2018; Bedny et al., 2019).

Neuroscientific studies suggest that thinking about visual categories engages similar neural systems across blind and sighted people (Koster-Hale et al., 2014; Noppeney et al., 2003; Bedny et al., 2012; Striem-Amit et al., 2018; Hauptman, Elli, et al., 2023). For example, blind and sighted adults activate overlapping neural circuits when thinking about colors and visual weather events such as ‘rainbow’ (Striem-Amit et al., 2018; Wang et al., 2020). Blind individuals make generative inferences about the beliefs of sighted people given their visual experiences and use typical neural circuits in the theory of mind network to make these inferences (Bedny et al., 2009; Koster-Hale et al., 2014). Blind individuals also have rich causal models of color and appearance, for instance distinguishing among artifacts for which color has an intentional purpose (e.g., paper, stop sign) and those for which it varies as a function of personal preference (e.g., mugs, hats) (Kim et al., 2021).

How do people who are born blind develop understanding of visual phenomena? Social learning via language is likely an important mechanism. The efficacy of language as a source of information about perception has recently been demonstrated by large language models. Like blind humans, these models successfully acquire information about the sensory world, including color similarity, object size, and the spatial layout of cities (e.g., Abdou et al., 2021; Marjieh et al., 2023; Gurnee & Tegmark, 2024). However, humans and large language models (LLMs) arrive at this knowledge in different ways. Insight into these differences emerges from one of the few examples of visual knowledge that is not shared across blind and sighted adults: the specific and often idiosyncratic colors of objects (e.g., polar bears are white, carrots are orange). Such knowledge is readily verbalizable, much more so than some other perceptual properties, like shape (Kim et al., 2019). LLMs generate canonical colors of objects that match the judgments of sighted adults (Abdou et al., 2021). By contrast, people who are blind show lower agreement with sighted adults about specific object colors and sometimes produce non-canonical responses (e.g., polar bears are black to retain warmth, carrots are green because of chlorophyll; Kim et al., 2019). Rather than memorize idiosyncratic color labels from language, as LLMs readily do, humans appear to use information encoded in linguistic input to build structured causal models that license inferences about object color. Unlike rote memorization, these inferences do not always result in ‘canonical’ responses. Together, this evidence suggests that the acquisition of visual knowledge in blindness depends on uniquely human forms of learning: social learning from linguistic evidence and causal reasoning.

3.1.2 Pluripotency of visual cortex in blindness

Plasticity in the visual system of people who are born blind is perhaps the most dramatic example of the cognitive pluripotency of cortical tissue. As discussed above, there is good reason to believe that visual cortices of humans are evolutionarily predisposed for vision (Krubitzer, 1995). Primary visual cortex located along the calcarine sulcus performs the first stage of cortical visual processing. V1 has an expanded ‘input’ layer IV and high neuronal density, possibly to enable fine-grained spatial resolution of visual perception (Collins et al., 2010). If specialization precluded flexibility, we would expect this part of the brain to resist functional change. Contrary to this prediction, visual cortices of people born blind take on non-visual functions, including braille reading, auditory localization, and decision making in auditory and tactile tasks (e.g., Sadato et al, 1996; Wanet-Defalque et al., 1988; Röder et al., 1996). Responses to non-visual tasks are observed throughout the visual hierarchy, from high level visual areas in the dorsal and ventral streams to primary visual cortex (e.g., Röder et al., 2002; Burton et al., 2003; Burton, 2003). Analogous functional changes are also observed in the auditory cortices of people who are born deaf (e.g., Finney et al., 2001; Hickok et al., 1997). For example, auditory cortices of people born deaf are sensitive to the meaning of visual animations (Zimmerman et al., in press).

The precise function of 'visual' areas in people who are born blind remains debated. Responses to non-visual stimuli in the visual cortices of blind people has been coined 'cross-modal' plasticity, reflecting the idea that cortical areas that evolved for one modality (i.e., vision) are 'repurposed' for processing information from other modalities (Bavelier & Neville, 2002; Pascual-Leone et al., 2005). For example, 'area MT+' responds preferentially to visual motion information in sighted people and to auditory motion information in people born blind (Poirier et al., 2006; Bedny et al., 2010; Wolbers et al., 2011).

However, much of the 'repurposing' of visual networks in people born blind does not appear to reflect 'modality switching.' In congenital blindness, different subnetworks of visual areas become specialized for different higher-order cognitive functions, including language, mathematical reasoning, braille reading, memory, and executive control (Röder et al., 2002; Sadato et al., 1996, 1998; Bedny et al., 2011; Crollen et al., 2019; Kanjlia et al., 2016; 2021; Abboud & Cohen, 2019). Activity in visual cortices of blind people is sensitive to abstract cognitive information, including the grammatical complexity of sentences and their meanings (Röder et al., 2002; Bedny et al., 2011; Lane et al., 2015). There is evidence that responses to higher-order cognitive processes in 'visual' cortices of blind people are behaviorally relevant. Transcranial magnetic stimulation applied to the visual cortex of blind individuals causes errors on non-visual tasks, including braille reading and verb generation (Cohen et al., 1997; Amedi et al., 2004; Kupers et al., 2007). Across individuals, activity in this region also correlates with sentence comprehension and verbal memory performance (Amedi et al., 2003, Lane et al., 2015). That visual networks of people born blind participate in higher-cognitive functions demonstrates the brain's capacity for substantial functional change—from low-level vision to higher-order cognition.

Importantly, such drastic changes in cortical function are only possible during development. Although some sensitivity to non-visual information is observed in the visual cortices of people who become blind as adults and even blindfolded sighted people, the most robust and systematic responses to non-visual information in visual cortices are found in people who are born blind (Cohen et al., 1999; Burton, 2003; Sadato et al., 2002; Bedny et al., 2012; Musz et al., 2022). This observation suggests that functional change in visual cortex is dependent on mechanisms of heightened plasticity in the developing brain (Hensch, 2004, 2005; Crair, et al., 1998).

Why and how do visual networks take on higher-cognitive functions? Exuberant connectivity appears to be a key part of the answer (Lewis et al., 2010; Bedny, 2017). Visual areas are connected with language networks in sighted and blind people (Saygin et al., 2016; Bedny et al., 2011). The visual system of sighted humans also receives rich 'top-down' connectivity from fronto-parietal networks involved in executive function (Bressler et al., 2008; Forkel et al., 2014). These connections support visual working memory and predictive perception (Baluch & Itti, 2011; Gilbert & Li, 2013). In people born blind, the same connections carry higher-cognitive information into visual cortex, enabling its incorporation into higher-cognitive systems.

Support for the role of top-down connectivity in visual cortex plasticity comes from studies of functional (resting-state) connectivity. In people born blind, visual networks show increased functional connectivity with higher-order cognitive systems in fronto-parietal cortices and decreased connectivity with sensory-motor auditory and tactile regions (e.g., Burton et al., 2014). This pattern suggests that the same anatomical structures function as sensory cortex for sighted people and as higher-cognitive cortex for people born blind. Patterns of functional specialization within visual cortex of congenitally blind individuals are predicted by resting-state connectivity with higher-cognitive networks. For example, areas of visual cortex that are most responsive to language show stronger connectivity with language networks (Bedny et al., 2011; Abboud & Cohen, 2019; Kanjlia et al., 2016, 2021). Elements of this 'blind' functional connectivity profile is present in sighted infants (Tian et al., 2023), suggesting that early visual experience shapes the later function of innate anatomical pathways.

It is interesting that the functions that primarily take over the visual cortices in blindness are higher-cognitive ones. Higher-cognitive functions, including language, appear to have the capacity to expand beyond their neural niche. This is likely due in part to the exuberant connectivity of higher-cognitive networks with the rest of the brain. The recruitment of visual networks for cultural skills in blindness is also notable. Some of the first illustrations of non-visual functions in the visual cortex of blind people came from studies of braille (e.g., Sadato et al., 1996, 1998). Other parts of visual cortex are engaged during mathematical tasks, exhibiting responses that scale with mathematical difficulty (Kanjlia et al., 2016). The visual system of people born blind responds more strongly to mathematics than to non-verbal numerical tasks (i.e., estimating numerosity of tone sequences) (Kanjlia et al., 2021). Together, this evidence suggests that behaviorally relevant cultural tools such as braille and math 'soak up' available cortical territory.

3.1.3 Summary of Blindness: Adaptation to sensory loss

Blindness illustrates several mechanisms of human adaptation. First, cortical areas exhibit peak sensitivity to experience early in life. Local cortical circuits that are evolutionarily predisposed for a particular cognitive function are nevertheless cognitively pluripotent (i.e., V1 repurposes for higher-order cognition). Exuberant connectivity is key to adaptation: connectivity between the visual system and higher-cognitive circuits enables 'higher-cognitive takeover' in blindness. Finally, humans adapt to sensory loss in uniquely human ways. The human ability to learn flexibly, including via social learning through language, and to build causal mental models using linguistic evidence, makes adaptation possible.

3.2 Language: An evolved, yet flexible social learning system

As noted above, the language system is an essential tool for social learning in humans (Pinker, 2010; Tooby & DeVore, 1987; Gelman, 2009). It is also a key example of how evolutionary preparedness coexists with flexibility. The language system exhibits multiple signatures of innate specification. These include i) commonalities in language use across humans, ii) resilient acquisition in childhood without explicit instruction, and iii) dedicated neurobiological machinery. Languages that are not historically linked share numerous commonalities, such as use of word order (e.g., SVO; English, Hmong Njua), grammatical gender (e.g., Dyirbal, German), and lexical tones (e.g., Mandarin, Cherokee) (Dryer, 2007; Comrie, 1999). Language acquisition unfolds effortlessly and follows a similar trajectory across children growing up in different linguistic communities (Gleitman & Newport, 1995; Clark & Casillas, 2015). Deaf children who do not have access to a sign language invent communication systems called 'homesign' that exhibit key features of natural languages (Goldin-Meadow, 2005). By contrast, attempts to teach our closest living ancestors (chimpanzees) language have proven unsuccessful (Terrace et al., 1979; Yang, 2013). A network of left-lateralized fronto-temporal brain regions exhibits high selectivity for language compared to other cognitive functions (Fedorenko et al., 2011; Malik-Moraleda et al., 2022; Bates et al., 1991; Hickok et al., 1996; Figure 3A). Several genes related to human language abilities have also been identified, including FOXP2, which is thought to have been the target of recent selection (Lai et al., 2001; Enard et al., 2002). Together, these observations suggest that linguistic representations are supported by an evolutionarily prepared neurobiological substrate.

At the same time, the language system itself shows evidence of adaptability. Although languages of the world share essential features, they are nonetheless more variable than the communication systems of other animals (e.g., Fischer & Price, 2017). It has been argued that no one set of linguistic features applies to all of the world's 5,000-8,000 languages, which vary widely at every level of linguistic representation (Evans & Levinson, 2009; Majid et al., 2018). Distinctive neural responses to linguistic stimuli across languages reflect this variation and offer evidence for flexibility in the neural basis of language (e.g., Xu et al., 2017; Chandrasekaran et al., 2007).

Critically, optimal language learning depends on early language experience (Lenneberg, 1967; Hartshorne et al., 2018; Gleitman & Newport, 1995). Learning a second language as an adult results in incomplete mastery (Hartshorne et al., 2018, Johnson & Newport, 1989). Delayed access to a first language has still more significant behavioral consequences (Mayberry & Kluender, 2018). The majority of deaf children (more than 90%) are born to hearing parents and have limited access to a fully accessible, visual-manual sign language early in life (Hall, 2017). Even subtle delays in access to a first language affect ultimate proficiency (e.g., Emmorey & Corina, 1990; Newport, 1990; MacSweeney et al., 2008b). Case studies with deaf adults who learned their first language in adolescence or early adulthood suggest that severely delayed access to language results in difficulties with grammar as well as altered neural responses to language (Woll, 2018; Ferjan-Ramirez et al., 2014; Cheng et al., 2019). The ability to fully harness the flexibility of the language system likely depends on heightened developmental plasticity and language access early in life.

A particularly compelling demonstration of neural adaptability and repurposing of connectivity is evidenced by variation in the modality of linguistic input. The vast majority of humans rely on audition to access language, yet hundreds of visual-manual sign languages are used by millions of people worldwide (Woll et al., 2001). Children exposed to a sign language from birth acquire language according to a similar developmental trajectory as children learning a spoken language, with manual babbling emerging in the second half of the first year and two-word phrases around age 2 (Lillo-Martin & Henner, 2021). Different sign languages such as American Sign Language (ASL), Libras, and Japanese Sign Language (JSL) each have a distinct phonology, morphology, and syntax (Perniss et al., 2007; Klima & Bellugi, 1979). While many grammatical structures are shared across different signed and spoken languages, such as topicalization and compounding, utilization of the visual modality enables sign language-specific grammatical devices, such as body anchoring, spatial referencing, and facial grammar (Emmorey, 2001; Reilly, 2006; Oomen & Kimmelman, 2019).

Sign language comprehension and production activate canonical left-lateralized fronto-temporal language regions, including the left inferior frontal and middle temporal gyri (Neville et al., 1997; Campbell et al., 2007; MacSweeney et al., 2008a; Emmorey, 2021; Richardson et al., 2020; Figure 3A). Sign language processing also elicits unique neural signatures. For example, visual cortex exhibits sensitivity to linguistic information when signers but not non-signers view ASL (Almeida et al., 2016; Brookshire et al., 2017), and the superior parietal lobule, which encodes spatial information, has been implicated in sign planning during production (Emmorey et al., 2016; Shum et al., 2020). Characterizing the neural responses specific to sign languages is an emerging line of inquiry in language neuroscience (Emmorey, 2021).

Visual reading provides another example of informational 'cross-talk' between the language and visual systems. We discuss this example of cultural adaptation in detail in the cultural symbol systems (Section 3.3) and therefore only briefly mention it here as it relates to the multi-modality of the language system. Why is the language system capable of interfacing with vision? According to one proposal, we can acquire visual-manual languages because language evolved from gestural communication (Corballis, 1999; Tomasello, 2010; McNeill, 2012; Pollick et al, 2007; Arbib et al., 2008). On this view, humans evolved to access language through vision.

While there may be a special link between language and vision, language also interfaces with touch. People who are DeafBlind use Protactile (PT) sign language, whereby locations on the body and continuous tactile feedback or 'backchanneling' are used to encode linguistic information (Clark, 2014; Granda & Nuccio, 2018). One case study suggests that DeafBlind individuals rely on fronto-temporal regions plus visual cortex during PT comprehension (Obretenova et al., 2010, Figure 3A). Braille, a reading system used by blind individuals, is another example of how language is accessed via touch. The blind French educator Louis Braille created the basic design of braille that is now used all over the world, which involves a two-column-by-three-row matrix of possible dot positions (Mellor, 2006). Braille is read by passing the finger rapidly across the raised dots, and blind adults can read upwards of 300 words per minute (Millar, 1984; 2003). Braille reading depends on a network of brain regions, including early somatosensory cortex and posterior parietal circuits, as well as 'visual' cortices, including but not limited to parts of the ventral occipito-temporal cortex that participate in visual reading (e.g., Sadato et al., 1996; Reich et al., 2011). Recent evidence suggests that people born blind may develop an anterior to posterior orthographic gradient that extends from early somatosensory to dorsal occipital and finally early visual occipital regions (Tian et al., 2023; Figure 3B).

Language is a key example of an evolutionarily prepared, domain-specific neurocognitive system that enables flexible social learning. The language network itself is also flexible: cortical pluripotency and enhanced developmental plasticity enable the acquisition of any natural language(s) during childhood. The exuberant connectivity of the language system to other networks makes it possible to acquire language in any modality. As discussed in the next section, this rich connectivity also allows language to contribute to many cultural technologies, such as reading, mathematics, and computer programming.

3.3 Cultural symbol systems: reading, math, and programming

Cultural symbol systems (reading, math, and programming) are a prime example of how human brains go beyond evolutionary predispositions. These systems have transformed human life, enabling the transmission of information across time and space, the design of modern technology, and most recently, the creation of artificial intelligence (AI) 'agents.' Yet, these tools were invented too recently for the brain to have evolved specific adaptations for their acquisition. For example, the earliest evidence of writing dates back to 3200 BCE (Schmandt-Besserat & Erard, 2008; de Voogt, 2021). Symbolic math and programming are even more recent inventions. Studies of how the human brain supports cultural symbol systems provide an important complementary perspective on human adaptation.

Unlike vision or language, reading, math, and programming require explicit instruction and are not acquired from birth. Literacy and symbolic number acquisition begins during the preschool years and continues throughout childhood into young adulthood. Learning to program often does not begin until late adolescence or adulthood, when many neural networks have reached maturity (Gogtay et al., 2004; Huttenlocher & Dabholkar, 1997). As a result, the degree of functional change in local cortical circuits during the acquisition of cultural symbol systems is likely subtler than in the case of sensory loss. Whether enhanced developmental plasticity plays any role in the neural basis of cultural symbol systems is not known. Like other examples of adaptation discussed previously, acquiring cultural symbol systems depends heavily on social learning via linguistic communication. Neurally, however, the fronto-temporal language network does not constitute the primary neural substrate of reading, math, or programming. Rather, all three cultural systems interface with language via the reuse of cross-network connectivity. As we discuss in detail below, both mathematics and programming additionally rely on domain-general reasoning systems.

We begin by discussing visual reading. The neural basis of visual reading is the best characterized of any cultural symbol system. Visual reading is also a distinctive form of adaptation, in that it involves the development of a novel perceptual 'entry-point' into the language system. Despite its evolutionarily recent invention, visual reading recruits common neuroanatomical mechanisms across people and languages in the left lateral ventral occipito-temporal cortex (vOTC) (Dehaene et al., 2002; Price et al., 1996; Purcell et al., 2011). The so-called visual word form area (VWFA) becomes specialized for written language relative to both spoken language and non-linguistic visual stimuli matched in visual complexity (e.g., false fonts) (Dehaene & Cohen, 2011; Szwed et al., 2011). Damage or electrical stimulation to this area interferes with the ability to read

(Hirshorn et al., 2016; Tsapkini & Rapp, 2010). The vOTC exhibits a spatial selectivity gradient, with the highest responses to letters, letter combinations, and words extending progressively from posterior to anterior regions (Vinckier et al., 2007) (Figure 3B). Critically, specialization for written symbols in vOTC emerges as a result of literacy and correlates with reading fluency in children and adults (Ben-Shachar et al., 2011; Dehaene-Lambertz et al., 2018).

Why does the VWFA develop in this canonical location? As discussed in the language section, one reason is connectivity. The VWFA is a part of the visual system that exhibits particularly strong connectivity with the language network, even prior to literacy (Saygin et al., 2016; Bouhali et al., 2014). It has also been suggested that reading 'recycles' domain-specific cortical maps predisposed by evolution to represent letter-like visual shapes (e.g., line-junctions), and orthographic systems have been modified over time to fit the processing capacities of the region (Dehaene & Cohen, 2007, 2011). Prior to literacy (i.e., in pre-literate children and illiterate adults), the anatomical location of the VWFA is involved in visual object recognition (Saygin et al., 2016; Dehaene-Lambertz et al., 2018). Reading therefore provides the best evidence of how neural resources that evolved for one 'domain-specific' function (visual object recognition) are subtly modified for a related, culturally constructed function (visual letter recognition). In the case of mathematics and programming, exactly how 'domain-specific' resources are modified to enable cultural recycling is less well understood, and domain-general resources also play a role.

Like reading, mathematics is a relatively recent human invention and is not culturally universal. Several languages lack words for large numbers. For example, Pirahã, a language spoken by the Pirahã people in the Amazonian rainforest, uses only three words to refer to approximate quantities: 'roughly one,' 'roughly two,' and 'many,' respectively (Frank et al., 2008; Gordon, 2004). Speakers of languages with few or no exact number words, like the Pirahã, perform differently on some exact number tasks compared to speakers of languages with exact number words (Boni et al., 2022; Spaepen et al., 2011; Frank et al., 2008; Gordon, 2004). This evidence suggests that linguistic and cultural experience influence numerical cognition.

Although language contributes to the development of exact numerical cognition, the fronto-temporal language system does not constitute the neural substrate of numerical or mathematical thinking (e.g., Cantlon et al., 2006; Piazza et al., 2007). Rather, a key neural system thought to provide the evolutionary and ontogenetic foundation is the so-called 'approximate number system,' which is implemented in fronto-parietal circuits (Brannon & Merritt, 2011; Cantlon & Brannon, 2007; Feigenson et al., 2004; Nieder, 2021a; Tudusciuc & Nieder, 2009). The approximate number system is evolutionarily ancient: species across the animal kingdom estimate numerical quantities (Brannon & Merritt, 2011; Cantlon & Brannon, 2007; Cantlon et al., 2009; Nieder, 2021a), and infants estimate quantities from birth (Xu et al., 2005; Feigenson et al., 2004). This system supports approximate arithmetic, including approximate addition and subtraction (Cantlon & Brannon, 2010). Unlike symbolic numerical thinking, such estimation is approximate and ratio-dependent. For example, it is just as easy to distinguish 5 from 10 and 50 from 100 dots, but harder to distinguish 90 from 100 dots (Brannon & Merritt, 2011; Nieder, 2021b).

In children, individual differences in approximate number estimation predict future math abilities (Libertus et al., 2011; Wang et al., 2017). Approximate number estimation and mathematics also recruit similar regions in fronto-parietal cortices (Amalric & Dehaene, 2018, 2019; Friedrich & Friederici, 2009; Kanjlia et al., 2016; Nakai & Sakai, 2014). For example, estimating numerosities of dots and tones (e.g., 4 vs. 8) can be decoded from patterns of neural activity in the human intra-parietal sulcus (IPS) (Damarla & Just, 2013; Eger et al., 2009; Kanjlia et al., 2021; Piazza & Eger, 2016). In non-human primates, neurons in the IPS are tuned to specific numerosities, with responses falling off as the number of dots or tones becomes more distant from their preferred numerosity (Nieder & Dehaene, 2009). Fronto-parietal networks are also active when adults and children solve math equations or make decisions about symbolic numbers (Amalric & Dehaene, 2019; Holloway et al., 2013; Kadosh et al., 2007; Maruyama et al., 2012). Similar networks are engaged when mathematicians consider the validity of highly abstract mathematical statements (Amalric & Dehaene, 2018; Amalric et al., 2018). Together, the evidence suggests that an evolved capacity for approximate numerical estimation contributes to the development of exact numerical thinking and mathematics.

However, the subtle modification and reuse of domain-specific neural representations of approximate number are unlikely to provide a full account of how the human brain enables exact numerical thinking or symbolic mathematics (Ansari, 2008). Although approximate number estimation is present from birth, children undergo a protracted process of learning the meanings of exact number words that takes years, suggesting substantial representational change (Carey & Barner, 2019; Spelke, 2017; Leslie et al., 2008). On the neural level, it is unclear how approximate neural tuning for numerosities gives rise to representations of exact symbolic numbers. There is evidence that neural representations of approximate and exact numbers in fronto-parietal cortex neighbor each other but are not the same: classifiers trained to distinguish neural (fMRI) patterns elicited during approximate number tasks (i.e., dot arrays) fail to distinguish neural patterns during digit-based tasks (Cavdaroglu et al., 2015; Eger et al., 2009). This evidence suggests that although approximate number representations contribute to the development of exact numerical thinking, the relationship between the two is complex and likely involves the recruitment of additional neurocognitive mechanisms.

Apart from their role in numerical approximation, fronto-parietal networks contribute to exact numerical and mathematical thinking because of their role in domain-general reasoning and symbol manipulation, which are central to numerical cognition (Anderson et al., 2014; Ansari, 2008). Domain-general fronto-parietal networks encode abstract hierarchical rule sets (Bunge et al., 2003; Bengtsson et al., 2009; Woolgar et al., 2016) and are engaged when reasoning about abstract variables devoid of concrete meaning (e.g., 'If X then Y') (Goel, 2007; Monti et al., 2009) as well as during non-verbal reasoning tasks such as Raven's Advanced Progressive Matrices (Raven, 1965; Prabhakaran et al., 1997; Xu et al., 2021; Fedorenko et al., 2013). Individual differences in core functions of domain-general fronto-parietal circuits, including executive control, working memory, and non-verbal reasoning, predict mathematical ability in children and adults (Clark et al., 2010; Cragg & Gilmore, 2014; Kyttälä & Lehto, 2008). There is also some evidence that neural responses to symbolic fractions in the IPS reflect domain-general cognitive processes rather than domain-specific responses to magnitude (Mock et al., 2019). Indeed, approximate number representations themselves may depend on domain-general rather than number-specific neural resources. For example, the IPS does not respond more to number approximation than to other non-quantification related tasks (Mock et al., 2019; Shuman & Kanwisher, 2004). Fronto-parietal domain-general reasoning networks contribute to symbolic math and exact numerical thinking.

The study of programming provides further evidence for the role of domain-general fronto-parietal reasoning networks in cultural symbol systems. Like mathematics, programming involves the manipulation of abstract symbols and the use of logical rules (e.g., IF conditional and FOR loops, as in chars = [x for x in "abcde" if x in "abracadabra"]). However, unlike mathematics, programming does not inherently involve quantity-related operations, although programs can refer to numerical data. Programming languages also make use of English words and recursive structures, akin to natural languages. Programming might therefore depend on the neural network that evolved for language (Fedorenko et al., 2019; Fitch et al., 2005; Prat et al., 2020; Siegmund et al., 2014). Contrary to this idea, programming, like mathematics, depends heavily on domain-general fronto-parietal reasoning networks.

Comprehension of programming code (including C, Python, Java, and Scratch) engages a domain-general fronto-parietal reasoning network (Liu et al., 2020; Ivanova et al., 2020; Floyd et al., 2017; Ikutani et al., 2021). Programming skills are predicted by deductive reasoning abilities and working memory capacity, but not linguistic skills (for review see Farghaly & El-Kafrawy, 2021). Neural responses to code comprehension in individual brains overlap with fronto-parietal responses to formal logical reasoning (e.g., identifying logical equivalence between statements such as, 'If both X and Y then not Z' and 'If Z then either not X or not Y') but not language comprehension (Liu et al., 2020; Monti et al., 2009). The fronto-parietal reasoning network is also involved in code generation (e.g., when participants type code or engage in covert code generation in the scanner) (Krueger et al., 2020; Xu et al., 2021). Patterns of activity in fronto-parietal reasoning networks encode the algorithms of code, such as FOR loops and IF conditionals (Ikutani et al., 2021; Liu et al., 2020; Srikant et al., 2022). This evidence suggests that the fronto-parietal reasoning network's propensity for representing rules and contingencies is recycled by the cultural phenomenon of programming (e.g., Bunge et al., 2003; Bengtsson et al., 2009; Woolgar et al., 2016).

The developmental origins of reasoning capacities remain an active area of investigation. Although human brains are prepared for reasoning, the degree to which cultural skills, such as programming and mathematics, recycle intrinsic capacities of fronto-parietal circuits or capacities that themselves are acquired earlier in childhood through learning remains to be fully understood. Fronto-parietal networks are engaged in logical reasoning in children as young as 6 years of age (Crone et al., 2009; Wright, Matlen, Baym, Ferrer, & Bunge, 2008). As mentioned above, fronto-parietal networks continue to mature anatomically and functionally for an extended period of time (Hartley et al., 2021; Werchan et al., 2016; Thompson-Schill et al., 2009). Little is known about the function of these systems in early infancy. There is some evidence that fronto-parietal systems are engaged in simple rule-learning in 8-month-old infants (Werchan et al, 2016; Raz & Saxe, 2020). Recent behavioral evidence suggests that preverbal infants engage in basic forms of logical reasoning, such as disjunctive syllogism deduction (Cesana-Arlotti, Kovács, & Téglás, 2020; Cesana-Arlotti et al., 2018; Feiman, Mody, & Carey, 2022). Emerging imaging studies with infants further suggest that despite their slow maturation, fronto-parietal circuits play a role in learning and inference from very early in life (Raz & Saxe, 2020).

In sum, cultural symbol systems, including reading, exact number and mathematics, and programming, depend on a combination of domain-specific and domain-general neural systems as well as their connectivity to each other and to perceptual systems (e.g., vision in the case of reading). Although the language network is not the primary neural substrate for any of the cultural symbol systems studied thus far, it nevertheless makes important contributions to them all. Reading is itself an alternative entry point to the language system, and visual reading depends on connectivity between language and visual object recognition circuitry. Exact numerical thinking and mathematics depends on language during learning. The language system also plays a supportive function in retrieving math facts from memory (Friedrich & Friederici, 2013; Maruyama et al., 2012). Likewise, most programming languages reuse linguistic symbols (e.g., words like 'for,' 'if,' and 'return') and some evidence suggests that the language network extracts 'gist' information during Python comprehension (Liu et al., 2024; Srikant et al., 2022). The human capacity to acquire cultural symbol systems is thus enabled in part by language and its interaction with other neural systems.

Summary and Discussion

Evidence from congenital sensory loss, language acquisition, and cultural skills offers a broad perspective on what makes humans so adaptable. Human brains embody a unique combination of specialization and flexibility. On the specialization side, we are equipped with evolutionarily prepared flexible learning systems that allow us to adapt efficiently to novel environments and situations. These systems are predisposed to support specific cognitive functions that enable powerful learning. One such evolutionarily prepared neurobiological system is language, which contributes to our capacity to learn from others. Domain-general reasoning networks likewise make us especially adept at flexible problem solving and contribute to our aptitude for culture.

At the same time, human adaptability is enabled not only by specific neurally prepared systems, but also by the functional flexibility of our neuroanatomy. Our brains are inherently malleable and can implement a variety of 'software' depending on the cognitive demands of the environment. How we use our neural wetware is heavily influenced by culture, our behavioral needs, the tools we use, what we choose to learn, and who we learn from.

Although humans are unusually flexible, we are not infinitely adaptable. The ease with which humans adapt to experience is partly explained by how that experience interacts with our mechanisms of adaptation. For example, we adapt more easily and more profoundly to early life experiences due to heightened plasticity during development (Hensch, 2004; 2005). Later experiences (e.g., literacy acquisition) build upon earlier ones (e.g., visual object recognition), leading to more subtle change. Although cognitive pluripotency of cortical circuits likely plays a role in all forms of behavioral adaptation, larger-scale differences in experience, such as total blindness from birth, make greater use of it. Finally, because social learning via language is a key adaptation mechanism, experiences that interfere with this 'adaptation machinery' are particularly hard to adapt to. For example, language deprivation among deaf children interferes with the ability to engage in social learning and is therefore more difficult to adapt to than deafness per se. Likewise, although people born blind adapt to a lack of vision, access to braille and accessible technology is paramount for full participation in literate and technology-driven societies.

We are just beginning to understand the neurobiological underpinnings of human adaptability. Many varieties of human experience remain unexamined or understudied (e.g., Mackey et al., 2013; Cetron et al., 2020). The phenomena that have received the most attention, such as reading and sensory loss, are unlikely to be representative. What neural mechanisms support culturally specific causal inferences, e.g., diseases are caused by viruses? Does medical expertise recycle domain-specific neurocognitive systems (e.g., intuitive biology) or instead rely on domain-general reasoning mechanisms? An exciting area of research not discussed in the current paper examines how the brain changes as a function of sociocultural norms (e.g., Kitayama & Park, 2010). We hypothesize that the adaptation mechanisms outlined in the current paper apply broadly, i.e., beyond the examples reviewed in this article, but this claim remains to be tested.

A further open question for future research is whether the adaptation mechanisms proposed in the current paper, such as cognitive pluripotency and exuberant connectivity, were specifically selected for in the human lineage because they enable flexible adaptation. Some prior work suggests that human brains are more plastic than those of other primates (Sherwood & Gomez-Robles, 2017). Future studies comparing adaptability across species could provide insight into such questions.

Figures

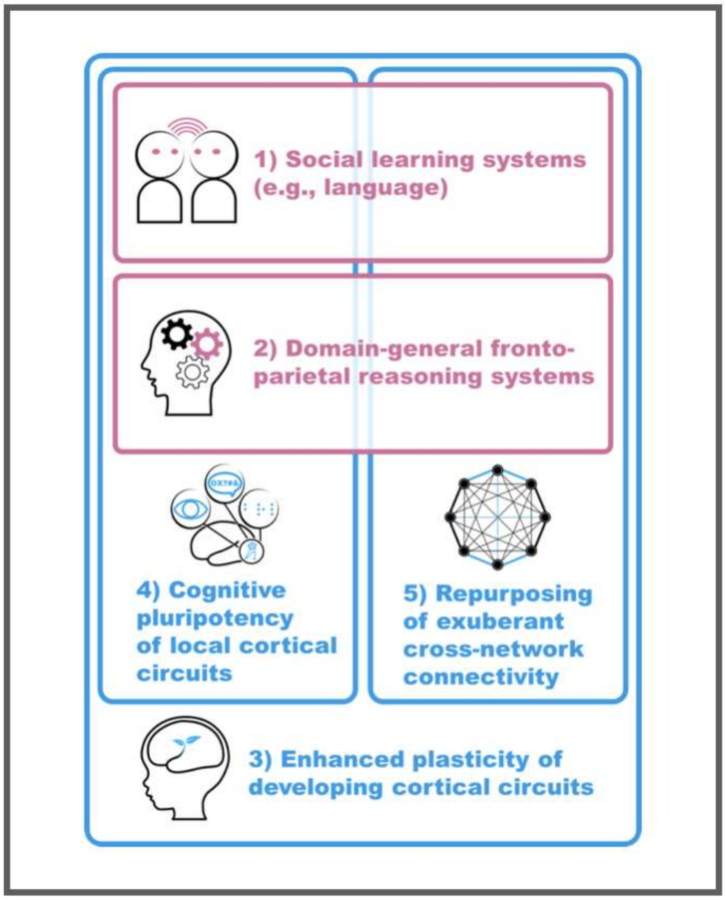

Figure 1. Mechanisms of adaptation according to the flexible specialization account. The mechanisms shown in pink (1, 2) are evolutionarily prepared neurocognitive systems that enable uniquely human flexible learning. The mechanisms shown in blue (3, 4, 5) are general mechanisms of functional plasticity.

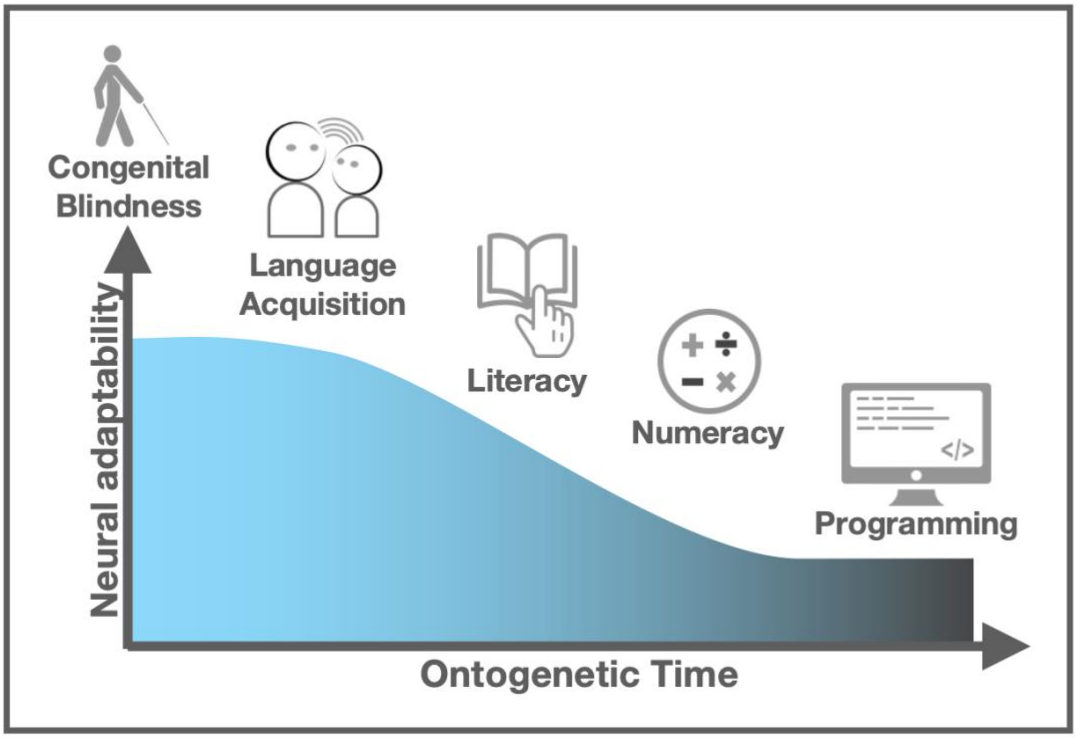

Figure 2. Experiential variation and neural adaptability. The developmental trajectory of the examples of experiential variation reviewed in the current article (congenital blindness, language acquisition, literacy, numeracy, programming) as well as how this trajectory lines up with the adaptability of the brain are shown.

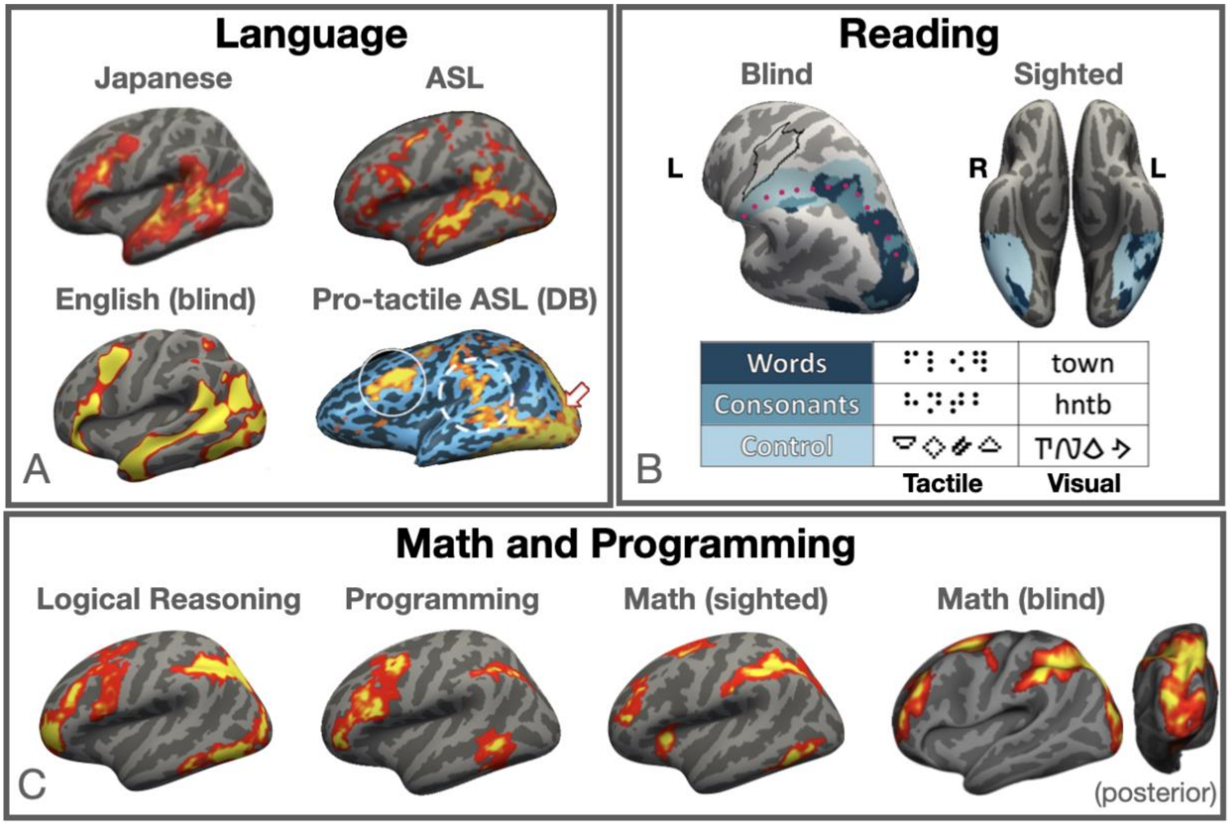

Figure 3. Examples of neural stability and adaptability across cognitive systems. Panel A: commonalities and differences in language network. Blindness leads to the additional recruitment of visual circuits for language processing (bottom row). Top-left: Japanese sentences > nonwords in one participant (Malik-Moraleda et al., 2022); top right: ASL > matched action videos in a deaf participant (unpublished data); bottom left: spoken English sentences > nonwords in a congenitally blind participant (Lane et al., 2015); bottom right: Protactile words > nonwords in a DeafBlind participant (Obretenova et al., 2010). Panel B: distinct reading streams in visual and braille reading (Tian et al., 2023). Panel C: similar neural responses to logical reasoning, programming, and math (blind and sighted) (Liu et al., 2020; Kanjlia et al., 2016). Blindness leads to the additional recruitment of visual circuits for math processing. Contrasts from left to right: logical reasoning > language, programming > working memory control, math equations > sentences.

Literature Cited

Abboud, S., & Cohen, L. (2019). Distinctive Interaction Between Cognitive Networks and the Visual Cortex in Early Blind Individuals. *Cerebral Cortex*, *29*(11), 4725–4742. https://doi.org/10.1093/cercor/bhz006

Abdou, M., Kulmizev, A., Hershcovich, D., Frank, S., Pavlick, E., & Søgaard, A. (2021). *Can Language Models Encode Perceptual Structure Without Grounding? A Case Study in Color* (arXiv:2109.06129). arXiv. https://doi.org/10.48550/arXiv.2109.06129

Almeida, D., Poeppel, D., & Corina, D. (2016). The processing of biologically plausible and implausible forms in American Sign Language: Evidence for perceptual tuning. *Language, Cognition and Neuroscience*, *31*(3), 361–374. https://doi.org/10.1080/23273798.2015.1100315

Amalric, M., & Dehaene, S. (2018). Cortical circuits for mathematical knowledge: evidence for a major subdivision within the brain's semantic networks. *Philosophical Transactions of the Royal Society B: Biological Sciences, 373*(1740), 20160515. doi:10.1098/rstb.2016.0515

Amalric, M., & Dehaene, S. (2019). A distinct cortical network for mathematical knowledge in the human brain. *NeuroImage, 189*, 19-31. doi:https://doi.org/10.1016/j.neuroimage.2019.01.001

Amalric, M., Denghien, I., & Dehaene, S. (2018). On the role of visual experience in mathematical development: Evidence from blind mathematicians. *Developmental Cognitive Neuroscience, 30*, 314-323. doi:https://doi.org/10.1016/j.dcn.2017.09.007

Amedi, A., Floel, A., Knecht, S., Zohary, E., & Cohen, L. G. (2004). Transcranial magnetic stimulation of the occipital pole interferes with verbal processing in blind subjects. *Nature Neuroscience*, *7*(11), 1266–1270. https://doi.org/10.1038/nn1328

Amedi, A., Raz, N., Pianka, P., Malach, R., & Zohary, E. (2003). Early 'visual' cortex activation correlates with superior verbal memory performance in the blind. *Nature Neuroscience*, *6*(7), 758–766. https://doi.org/10.1038/nn1072

Amunts, K., & Zilles, K. (2015). Architectonic mapping of the human brain beyond Brodmann. Neuron, 88(6), 1086-1107.

Anderson, J. R., Lee, H. S., & Fincham, J. M. (2014). Discovering the structure of mathematical problem solving. *NeuroImage, 97*, 163-177.

Anderson, M. L. (2010). Neural reuse: A fundamental organizational principle of the brain. *Behavioral and Brain Sciences*, *33*(4), 245–266. https://doi.org/10.1017/S0140525X10000853

Ansari, D. (2008). Effects of development and enculturation on number representation in the brain. Nature Reviews Neuroscience, 9(4), 278-291. doi:10.1038/nrn2334

Arbib, M. A., Liebal, K., & Pika, S. (2008). Primate Vocalization, Gesture, and the Evolution of Human Language. *Current Anthropology*, *49*(6), 1053–1076. https://doi.org/10.1086/593015

Badre, D., & Nee, D. E. (2018). Frontal cortex and the hierarchical control of behavior. *Trends in cognitive sciences*, *22*(2), 170-188.

Badre, D., Kayser, A. S., & D'Esposito, M. (2010). Frontal cortex and the discovery of abstract action rules. *Neuron*, *66*(2), 315-326.

Baluch, F., & Itti, L. (2011). Mechanisms of top-down attention. *Trends in Neurosciences*, *34*(4), 210–224. https://doi.org/10.1016/j.tins.2011.02.003

Barnes, E. (2016). *The minority body: A theory of disability*. Oxford University Press.

Barsalou, L. W. (1999). Perceptual symbol systems. *Behavioral and Brain Sciences*, *22*(4), 577–660. https://doi.org/10.1017/S0140525X99002149

Bates, E., Wulfeck, B., & MacWhinney, B. (1991). Cross-linguistic research in aphasia: An overview. *Brain and Language*, *41*(2), 123–148. https://doi.org/10.1016/0093-934X(91)90149-U

Bavelier, D., & Neville, H. J. (2002). Cross-modal plasticity: Where and how? *Nature Reviews Neuroscience*, *3*(6), 443–452. https://doi.org/10.1038/nrn848

Bedny, M. (2017). Evidence from Blindness for a Cognitively Pluripotent Cortex. *Trends in Cognitive Sciences*, *21*(9), 637–648. https://doi.org/10.1016/j.tics.2017.06.003

Bedny, M., Caramazza, A., Pascual-Leone, A., & Saxe, R. (2012). Typical Neural Representations of Action Verbs Develop without Vision. *Cerebral Cortex*, *22*(2), 286–293. https://doi.org/10.1093/cercor/bhr081

Bedny, M., Konkle, T., Pelphrey, K., Saxe, R., & Pascual-Leone, A. (2010). Sensitive Period for a Multimodal Response in Human Visual Motion Area MT/MST. *Current Biology*, *20*(21), 1900–1906. https://doi.org/10.1016/j.cub.2010.09.044

Bedny, M., Koster-Hale, J., Elli, G., Yazzolino, L., & Saxe, R. (2019). There’s more to ‘sparkle’ than meets the eye: Knowledge of vision and light verbs among congenitally blind and sighted individuals. *Cognition*, *189*, 105–115.

Bedny, M., Pascual-Leone, A., & Saxe, R. R. (2009). Growing up blind does not change the neural bases of Theory of Mind. *Proceedings of the National Academy of Sciences*, *106*(27), 11312–11317. https://doi.org/10.1073/pnas.0900010106

Bedny, M., Pascual-Leone, A., Dodell-Feder, D., Fedorenko, E., & Saxe, R. (2011). Language processing in the occipital cortex of congenitally blind adults. *Proceedings of the National Academy of Sciences*, *108*(11), 4429–4434. https://doi.org/10.1073/pnas.1014818108

Bellugi, U., Poizner, H., & Klima, E. S. (1989). Language, modality and the brain. Trends in neurosciences, 12(10), 380-388.

Benedict, R. (1935). Patterns of culture. Routledge.

Ben-Shachar, M., Dougherty, R. F., Deutsch, G. K., & Wandell, B. A. (2011). The development of cortical sensitivity to visual word forms. *Journal of Cognitive Neuroscience, 23*(9), 2387-2399.

Bengtsson, S. L., Haynes, J.-D., Sakai, K., Buckley, M. J., & Passingham, R. E. (2009). The representation of abstract task rules in the human prefrontal cortex. Cerebral Cortex, 19(8), 1929-1936.

Bigelow, A. (1987). Early words of blind children. *Journal of Child Language*. 1987;14(1):47-56. doi:10.1017/S0305000900012721

Boni, I., Jara-Ettinger, J., Sackstein, S., & Piantadosi, S. T. (2022). Verbal counting and the timing of number acquisition in an indigenous Amazonian group. *PLoS ONE, 17*(8), e0270739.

Boas, F. (1896). The limitations of the comparative method of anthropology. *Science*, *4*(103), 901-908.

Bongard, S., & Nieder, A. (2010). Basic mathematical rules are encoded by primate prefrontal cortex neurons. Proceedings of the National Academy of Sciences, 107(5), 2277-2282.

Bouhali, F., Thiebaut de Schotten, M., Pinel, P., Poupon, C., Mangin, J.-F., Dehaene, S., & Cohen, L. (2014). Anatomical Connections of the Visual Word Form Area. The Journal of Neuroscience, 34(46), 15402-15414. doi:10.1523/jneurosci.4918-13.2014

Boyd, R., Richerson, P. J., & Henrich, J. (2011). The cultural niche: Why social learning is essential for human adaptation. *Proceedings of the National Academy of Sciences*, *108*(supplement_2), 10918–10925. https://doi.org/10.1073/pnas.1100290108

Brannon, E. M., & Merritt, D. J. (2011). Evolutionary foundations of the approximate number system. *Space, time and number in the brain*, 207-224.

Bressler, S. L., Tang, W., Sylvester, C. M., Shulman, G. L., & Corbetta, M. (2008). Top-Down Control of Human Visual Cortex by Frontal and Parietal Cortex in Anticipatory Visual Spatial Attention. *The Journal of Neuroscience*, *28*(40), 10056–10061. https://doi.org/10.1523/JNEUROSCI.1776-08.2008

Brookshire, G., Lu, J., Nusbaum, H. C., Goldin-Meadow, S., & Casasanto, D. (2017). Visual cortex entrains to sign language. *Proceedings of the National Academy of Sciences*, *114*(24), 6352–6357. https://doi.org/10.1073/pnas.1620350114

Bullmore, E., & Sporns, O. (2012). The economy of brain network organization. *Nature Reviews Neuroscience*, *13*(5), 336–349. https://doi.org/10.1038/nrn3214

Bunge, S. A., Kahn, I., Wallis, J. D., Miller, E. K., & Wagner, A. D. (2003). Neural circuits subserving the retrieval and maintenance of abstract rules. Journal of neurophysiology, 90(5), 3419-3428.

Burton, H. (2003). Visual Cortex Activity in Early and Late Blind People. *The Journal of Neuroscience*, *23*(10), 4005–4011. https://doi.org/10.1523/JNEUROSCI.23-10-04005.2003

Burton, H., Diamond, J. B., & McDermott, K. B. (2003). Dissociating Cortical Regions Activated by Semantic and Phonological Tasks: A fMRI Study in Blind and Sighted People. *Journal of Neurophysiology*, *90*(3), 1965–1982. https://doi.org/10.1152/jn.00279.2003

Burton, H., Snyder, A. Z., & Raichle, M. E. (2014). Resting state functional connectivity in early blind humans. *Frontiers in Systems Neuroscience*, *8*. https://doi.org/10.3389/fnsys.2014.00051

Campbell, E. E., & Bergelson, E. (2022). Making sense of sensory language: Acquisition of sensory knowledge by individuals with congenital sensory impairments. *Neuropsychologia*, *174*, 108320.

Campbell, E., Casillas, R., & Bergelson, E. (2024). The role of vision in the acquisition of words: Vocabulary development in blind toddlers. Developmental Science, e13475.

Campbell, R., MacSweeney, M., & Waters, D. (2007). Sign Language and the Brain: A Review. *Journal of Deaf Studies and Deaf Education*, *13*(1), 3–20. https://doi.org/10.1093/deafed/enm035

Cantlon, J. F., & Brannon, E. M. (2007). Basic Math in Monkeys and College Students. *PLOS Biology, 5*(12), e328. doi:10.1371/journal.pbio.0050328

Cantlon, J. F., & Brannon, E. M. (2010). Animal arithmetic. In N. Clayton (Ed.), Encyclopedia of Animal Behavior. Oxford: Elsevier.

Cantlon, J. F., Brannon, E. M., Carter, E. J., & Pelphrey, K. A. (2006). Functional imaging of numerical processing in adults and 4-y-old children. PLoS biology, 4(5), e125.

Cantlon, J. F., Libertus, M. E., Pinel, P., Dehaene, S., Brannon, E. M., & Pelphrey, K. A. (2009). The Neural Development of an Abstract Concept of Number. Journal of Cognitive Neuroscience, 21(11), 2217-2229. doi:10.1162/jocn.2008.21159

Carey, S., & Barner, D. (2019). Ontogenetic origins of human integer representations. *Trends in Cognitive Sciences, 23*(10), 823-835.

Carey, S. (2009). The origin of concepts: Oxford university press.

Carrigan, E. M., & Coppola, M. (2017). Successful communication does not drive language development: Evidence from adult homesign. *Cognition*, *158*, 10–27. https://doi.org/10.1016/j.cognition.2016.09.012

Cavdaroglu, S., Katz, C., & Knops, A. (2015). Dissociating estimation from comparison and response eliminates parietal involvement in sequential numerosity perception. *NeuroImage, 116*, 135-148.

Cesana-Arlotti, N., Kovács, Á. M., & Téglás, E. (2020). Infants recruit logic to learn about the social world. Nature Communications, 11(1), 5999.

Cesana-Arlotti, N., Martín, A., Téglás, E., Vorobyova, L., Cetnarski, R., & Bonatti, L. L. (2018). Precursors of logical reasoning in preverbal human infants. *Science, 359*(6381), 1263-1266.

Cetron, J. S., Connolly, A. C., Diamond, S. G., May, V. V., Haxby, J. V., & Kraemer, D. J. M. (2020). Using the force: STEM knowledge and experience construct shared neural representations of engineering concepts. NPJ science of learning, 5(1), 6. doi:10.1038/s41539-020-0065-x

Chandrasekaran, B., Krishnan, A., & Gandour, J. T. (2007). Mismatch negativity to pitch contours is influenced by language experience. *Brain Research*, *1128*, 148–156. https://doi.org/10.1016/j.brainres.2006.10.064

Cheng, Q., Roth, A., Halgren, E., & Mayberry, R. I. (2019). Effects of early language deprivation on brain connectivity: Language pathways in deaf native and late first-language learners of American Sign Language. *Frontiers in Human Neuroscience*, *13*, 320.

Chomsky, N. (1965). Aspects of the Theory of Syntax (No. 11). MIT press.

Clark, C. A., Pritchard, V. E., & Woodward, L. J. (2010). Preschool executive functioning abilities predict early mathematics achievement. *Developmental psychology, 46*(5), 1176.

Clark, E. V., & Casillas, M. (2015). First language acquisition. In *The Routledge handbook of linguistics* (pp. 311-328). Routledge.

Clark, J. L. (2014). *Where I stand: On the signing community and my DeafBlind experience*. Handtype Press.

Coetzee, J., & Monti, M. (2018). At the core of reasoning: Dissociating deductive and non-deductive load. *Human Brain Mapping, 39*(4), 1850-1861. doi:10.1002/hbm.23979

Cohen, L. G., Celnik, P., Pascual-Leone, A., Corwell, B., Faiz, L., Dambrosia, J., Honda, M., Sadato, N., Gerloff, C., Dolores Catala, M., & Hallett, M. (1997). Functional relevance of cross-modal plasticity in blind humans. *Nature*, *389*(6647), 180-183.

Cohen, L. G., Weeks, R. A., Sadato, N., Celnik, P., Ishii, K., & Hallett, M. (1999). Period of susceptibility for cross-modal plasticity in the blind. *Annals of Neurology*, *45*(4), 451–460. https://doi.org/10.1002/1531-8249(199904)45:4<451::AID-ANA6>3.0.CO;2-B

Collignon, O., Voss, P., Lassonde, M., & Lepore, F. (2009). Cross-modal plasticity for the spatial processing of sounds in visually deprived subjects. *Experimental brain research*, *192*, 343-358.
Fedorenko, E., & Varley, R. (2016). Language and thought are not the same thing: evidence from neuroimaging and neurological patients. *Annals of the New York Academy of Sciences*, *1369*(1), 132-153.

Collins, C. E., Airey, D. C., Young, N. A., Leitch, D. B., & Kaas, J. H. (2010). Neuron densities vary across and within cortical areas in primates. *Proceedings of the National Academy of Sciences*, *107*(36), 15927–15932. https://doi.org/10.1073/pnas.1010356107

Comrie, B. (1999). Grammatical gender systems: a linguist's assessment. *Journal of Psycholinguistic research*, *28*, 457-466.

Corballis, M. C. (1999). The Gestural Origins of Language: Human language may have evolved from manual gestures, which survive today as a “behavioral fossil” coupled to speech. *American Scientist*, *87*(2), 138–145.

Cragg, L., & Gilmore, C. (2014). Skills underlying mathematics: The role of executive function in the development of mathematics proficiency. *Trends in Neuroscience and Education, 3*(2), 63-68.

Crair, M. C., Gillespie, D. C., & Stryker, M. P. (1998). The Role of Visual Experience in the Development of Columns in Cat Visual Cortex. *Science*, *279*(5350), 566–570. https://doi.org/10.1126/science.279.5350.566

Crollen, V., Lazzouni, L., Rezk, M., Bellemare, A., Lepore, F., Noël, M.-P., Seron, X., & Collignon, O. (2019). Recruitment of the occipital cortex by arithmetic processing follows computational bias in the congenitally blind. *NeuroImage*, *186*, 549–556. https://doi.org/10.1016/j.neuroimage.2018.11.034

Crone, E. A., Wendelken, C., Van Leijenhorst, L., Honomichl, R. D., Christoff, K., & Bunge, S. A. (2009). Neurocognitive development of relational reasoning. *Developmental Science, 12*(1), 55-66. doi:https://doi.org/10.1111/j.1467-7687.2008.00743.x

Damarla, S. R., & Just, M. A. (2013). Decoding the representation of numerical values from brain activation patterns. *Human Brain Mapping, 34*(10), 2624-2634.

Danker, J. F., & Anderson, J. R. (2007). The roles of prefrontal and posterior parietal cortex in algebra problem solving: A case of using cognitive modeling to inform neuroimaging data. *Neuroimage*, *35*(3), 1365-1377.

Deen, B., Richardson, H., Dilks, D. D., Takahashi, A., Keil, B., Wald, L. L., Kanwisher, N., & Saxe, R. (2017). Organization of high-level visual cortex in human infants. *Nature Communications*, *8*(1), 13995. https://doi.org/10.1038/ncomms13995

Deen, B., Saxe, R., & Bedny, M. (2015). Occipital Cortex of Blind Individuals Is Functionally Coupled with Executive Control Areas of Frontal Cortex. *Journal of Cognitive Neuroscience*, *27*(8), 1633–1647. https://doi.org/10.1162/jocn_a_00807

Dehaene-Lambertz, G., Monzalvo, K., & Dehaene, S. (2018). The emergence of the visual word form: Longitudinal evolution of category-specific ventral visual areas during reading acquisition. *PLOS Biology, 16*(3), e2004103. doi:10.1371/journal.pbio.2004103

Dehaene, S., & Cohen, L. (2007). Cultural recycling of cortical maps. *Neuron, 56*(2), 384-398. doi:https://doi.org/10.1016/j.neuron.2007.10.004

Dehaene, S., & Cohen, L. (2011). The unique role of the visual word form area in reading. Trends in Cognitive Sciences, 15(6), 254-262. doi:https://doi.org/10.1016/j.tics.2011.04.003

Dehaene, S., Le Clec'H, G., Poline, J.-B., Le Bihan, D., & Cohen, L. (2002). The visual word form area: a prelexical representation of visual words in the fusiform gyrus. *Neuroreport, 13*(3), 321-325. doi:https://doi.org/10.1097/00001756-200203040-00015

de Voogt, A. (2021). The Evolution of Writing Systems: An Introduction Oxford Handbook of Human Symbolic Evolution (pp. 0): Oxford University Press. Retrieved from https://doi.org/10.1093/oxfordhb/9780198813781.013.35.

Dryer, M. S. (2007). Word order. *Language typology and syntactic description*, *1*(61-131), 1-1.

Duncan, J. (2010). The multiple-demand (MD) system of the primate brain: mental programs for intelligent behaviour. *Trends in Cognitive Sciences, 14*(4), 172-179. doi:https://doi.org/10.1016/j.tics.2010.01.004

Dunlea, A. (1989). *Vision and the emergence of meaning: Blind and sighted children's early language*. Cambridge University Press.

Durkheim, E. (1947). *The Division of Labor in Society*, tr. George Simpson (New York).

Eger, E., Michel, V., Thirion, B., Amadon, A., Dehaene, S., & Kleinschmidt, A. (2009). Deciphering cortical number coding from human brain activity patterns. *Current Biology, 19*(19), 1608-1615. doi:https://doi.org/10.1016/j.cub.2009.08.047

Eiselt, A.-K., & Nieder, A. (2013). Representation of abstract quantitative rules applied to spatial and numerical magnitudes in primate prefrontal cortex. Journal of Neuroscience, 33(17), 7526-7534.

Emmorey, K. (2001). Space on hand: The exploitation of signing space to illustrate abstract thought. In M. Gattis (Ed.), *Spatial schemas and abstract thought* (pp. 147–174). The MIT Press.

Emmorey, K. (2021). New Perspectives on the Neurobiology of Sign Languages. *Frontiers in Communication*, *6*. https://doi.org/10.3389/fcomm.2021.748430

Emmorey, K., & Corina, D. (1990). Lexical Recognition in Sign Language: Effects of Phonetic Structure and Morphology. *Perceptual and Motor Skills*, *71*(3_suppl), 1227–1252. https://doi.org/10.2466/pms.1990.71.3f.1227

Emmorey, K., Mehta, S., McCullough, S., & Grabowski, T. J. (2016). The neural circuits recruited for the production of signs and fingerspelled words. *Brain and Language*, *160*, 30–41. https://doi.org/10.1016/j.bandl.2016.07.003

Enard, W., Przeworski, M., Fisher, S. E., Lai, C. S. L., Wiebe, V., Kitano, T., Monaco, A. P., & Pääbo, S. (2002). Molecular evolution of FOXP2, a gene involved in speech and language. *Nature*, *418*(6900), 869–872. https://doi.org/10.1038/nature01025

Epstein, R. A., Parker, W. E., & Feiler, A. M. (2007). Where Am I Now? Distinct Roles for Parahippocampal and Retrosplenial Cortices in Place Recognition. *Journal of Neuroscience*, *27*(23), 6141–6149. https://doi.org/10.1523/JNEUROSCI.0799-07.2007

Epstein, R., & Kanwisher, N. (1998). A cortical representation of the local visual environment. *Nature*, *392*(6676), 598-601.

Espinosa, J. S., & Stryker, M. P. (2012). Development and Plasticity of the Primary Visual Cortex. *Neuron*, *75*(2), 230–249. https://doi.org/10.1016/j.neuron.2012.06.009

Evans, N., & Levinson, S. C. (2009). The myth of language universals: Language diversity and its importance for cognitive science. *Behavioral and Brain Sciences*, *32*(5), 429–448. https://doi.org/10.1017/S0140525X0999094X

Farghaly, A. A., & El-Kafrawy, P. M. (2021). Exploring The Use Of Cognitive Tests To Predict Programming Performance: A Systematic Literature Review. Paper presented at the 2021 31st International Conference on Computer Theory and Applications (ICCTA). https://doi.org/10.1109/ICCTA54562.2021.9916610

Fedorenko, E., Behr, M. K., & Kanwisher, N. (2011). Functional specificity for high-level linguistic processing in the human brain. *Proceedings of the National Academy of Sciences*, *108*(39), 16428–16433. https://doi.org/10.1073/pnas.1112937108

Fedorenko, E., Duncan, J., & Kanwisher, N. (2013). Broad domain generality in focal regions of frontal and parietal cortex. *Proceedings of the National Academy of Sciences, 110*(41), 16616-16621. doi:10.1073/pnas.1315235110

Fedorenko, E., Ivanova, A., Dhamala, R., & Bers, M. U. (2019). The language of programming: a cognitive perspective. *Trends in Cognitive Sciences*. doi:https://doi.org/10.1016/j.tics.2019.04.010

Feigenson, L., Dehaene, S., & Spelke, E. (2004). Core systems of number. *Trends in Cognitive Sciences, 8*(7), 307-314. doi:https://doi.org/10.1016/j.tics.2004.05.002

Feiman, R., Mody, S., & Carey, S. (2022). The development of reasoning by exclusion in infancy. *Cognitive Psychology, 135*, 101473.

Ferjan-Ramirez, N., Leonard, M. K., Torres, C., Hatrak, M., Halgren, E., & Mayberry, R. I. (2014). Neural Language Processing in Adolescent First-Language Learners. *Cerebral Cortex*, *24*(10), 2772–2783. https://doi.org/10.1093/cercor/bht137

Finney, E. M., Fine, I., & Dobkins, K. R. (2001). Visual stimuli activate auditory cortex in the deaf. *Nature Neuroscience*, *4*(12), 1171–1173. https://doi.org/10.1038/nn763

Fischer, J., & Price, T. (2017). Meaning, intention, and inference in primate vocal communication. *Neuroscience & Biobehavioral Reviews*, *82*, 22-31.

Fitch, W. T., Hauser, M. D., & Chomsky, N. (2005). The evolution of the language faculty: clarifications and implications. *Cognition, 97*(2), 179-210.

Floyd, B., Santander, T., & Weimer, W. (2017). Decoding the representation of code in the brain: An fMRI study of code review and expertise. Paper presented at the Proceedings of the 39th International Conference on Software Engineering.

Forkel, S. J., Thiebaut de Schotten, M., Kawadler, J. M., Dell'Acqua, F., Danek, A., & Catani, M. (2014). The anatomy of fronto-occipital connections from early blunt dissections to contemporary tractography. *Cortex*, *56*, 73–84. https://doi.org/10.1016/j.cortex.2012.09.005

Frank, M. C., Everett, D. L., Fedorenko, E., & Gibson, E. (2008). Number as a cognitive technology: Evidence from Pirahã language and cognition. *Cognition, 108*(3), 819-824.

Friederici, A. D. (2009). Pathways to language: Fiber tracts in the human brain. *Trends in Cognitive Sciences*, *13*(4), 175–181. https://doi.org/10.1016/j.tics.2009.01.001

Friedrich, R. M., & Friederici, A. D. (2009). Mathematical logic in the human brain: syntax. *PLoS ONE, 4*(5), e5599. doi:10.1371/journal.pone.0005599

Friedrich, R. M., & Friederici, A. D. (2013). Mathematical logic in the human brain: semantics. *PLoS ONE, 8*(1), e53699. doi:10.1371/journal.pone.0053699

Gallese, V., & Lakoff, G. (2005). The Brain's concepts: The role of the Sensory-motor system in conceptual knowledge. *Cognitive Neuropsychology*, *22*(3–4), 455–479. https://doi.org/10.1080/02643290442000310

Gelman, S. A. (2009). Learning from Others: Children's Construction of Concepts. *Annual Review of Psychology*, *60*(1), 115–140. https://doi.org/10.1146/annurev.psych.59.103006.093659

Gilbert, C. D., & Li, W. (2013). Top-down influences on visual processing. *Nature Reviews Neuroscience*, *14*(5), 350–363. https://doi.org/10.1038/nrn3476

Gleitman, L., & Newport, E. (1995). The invention of language by children: Environmental and biological influences on the acquisition of language. In Gleitman, L., & Liberman, M. (Eds.), Language: An invitation to cognitive science (2nd edition). Cambridge, MA: MIT Press.

Goel, V. (2007). Anatomy of deductive reasoning. *Trends in Cognitive Sciences, 11*(10), 435-441. doi:https://doi.org/10.1016/j.tics.2007.09.003

Gogtay, N., Giedd, J. N., Lusk, L., Hayashi, K. M., Greenstein, D., Vaituzis, A. C., ... & Thompson, P. M. (2004). Dynamic mapping of human cortical development during childhood through early adulthood. *Proceedings of the National Academy of Sciences*, *101*(21), 8174-8179.

Goldin-Meadow, S. (2005). *The resilience of language: What gesture creation in deaf children can tell us about how all children learn language*. Psychology Press.

Gopnik, A., & Wellman, H. M. (1992). Why the child's theory of mind really is a theory. *Mind & Language, 7*(1– 2), 145–171.

Gordon, P. (2004). Numerical cognition without words: Evidence from Amazonia. Science, 306(5695), 496-499.

Granda, A., & Nuccio, J. (2018). Protactile principles. *Monmouth, OR: Tactile Communications*.

Greenough, W. T., Black, J. E., & Wallace, C. S. (1987). Experience and brain development. *Child development*, 539-559.

Grill-Spector, K., & Malach, R. (2004). The Human Visual Cortex. *Annual Review of Neuroscience*, *27*(1), 649–677. https://doi.org/10.1146/annurev.neuro.27.070203.144220

Gurnee, W., & Tegmark, M. (2024). *Language Models Represent Space and Time* (arXiv:2310.02207). arXiv. http://arxiv.org/abs/2310.02207

Gweon, H. (2021). Inferential social learning: Cognitive foundations of human social learning and teaching. Trends in cognitive sciences, 25(10), 896-910.

Hall, W. C. (2017). What You Don't Know Can Hurt You: The Risk of Language Deprivation by Impairing Sign Language Development in Deaf Children. Maternal and Child Health Journal, 21(5), 961–965. https://doi.org/10.1007/s10995-017-2287-y

Harris, P. L., & Koenig, M. A. (2006). Trust in testimony: How children learn about science and religion. *Child development*, *77*(3), 505-524.

Hartley, C. A. (2022). How do natural environments shape adaptive cognition across the lifespan?. Trends in Cognitive Sciences, 26(12), 1029-1030.

Hartley, C. A., Nussenbaum, K., & Cohen, A. O. (2021). Interactive development of adaptive learning and memory. Annual Review of Developmental Psychology, 3, 59-85.

Hartshorne, J. K., Tenenbaum, J. B., & Pinker, S. (2018). A critical period for second language acquisition: Evidence from 2/3 million English speakers. *Cognition*, *177*, 263–277. https://doi.org/10.1016/j.cognition.2018.04.007

Hauptman, M., Elli, G., Pant, R., & Bedny, M. (2023). Neural specialization for 'visual'concepts emerges in the absence of vision. *bioRxiv*.

Hauser, M. D., Chomsky, N., & Fitch, W. T. (2002). The Faculty of Language: What Is It, Who Has It, and How Did It Evolve? *Science*, *298*(5598), 1569–1579. https://doi.org/10.1126/science.298.5598.1569

Henrich, J., & McElreath, R. (2003). The evolution of cultural evolution. *Evolutionary Anthropology: Issues, News, and Reviews*, *12*(3), 123–135. https://doi.org/10.1002/evan.10110

Hensch, T. K. (2004). Critical Period Regulation. *Annual Review of Neuroscience*, *27*(1), 549–579. https://doi.org/10.1146/annurev.neuro.27.070203.144327

Hensch, T. K. (2005). Critical period plasticity in local cortical circuits. *Nature Reviews Neuroscience*, *6*(11), 877–888. https://doi.org/10.1038/nrn1787

Hensch, T. K. (2018). Critical periods in cortical development. In *The neurobiology of brain and behavioral development* (pp. 133-151). Academic Press.

Heyes, C. (2018). *Cognitive gadgets: The cultural evolution of thinking*. Harvard University Press.

Hickok, G., Bellugi, U., & Klima, E. S. (1996). The neurobiology of sign language and its implications for the neural basis of language. *Nature*, *381*(6584), 699–702. https://doi.org/10.1038/381699a0

Hickok, G., Poeppel, D., Clark, K., Buxton, R. B., Rowley, H. A., & Roberts, T. P. L. (1997). Sensory mapping in a congenitally deaf subject: MEG and fRMI studies of cross-modal non-plasticity. *Human Brain Mapping*, *5*(6), 437–444. https://doi.org/10.1002/(SICI)1097-0193(1997)5:6<437::AID-HBM4>3.0.CO;2-4

Hirshorn, E. A., Li, Y., Ward, M. J., Richardson, R. M., Fiez, J. A., & Ghuman, A. S. (2016). Decoding and disrupting left midfusiform gyrus activity during word reading. *Proceedings of the National Academy of Sciences, 113*(29), 8162-8167.

Holloway, I. D., Battista, C., Vogel, S. E., & Ansari, D. (2013). Semantic and perceptual processing of number symbols: evidence from a cross-linguistic fMRI adaptation study. Journal of Cognitive Neuroscience, 25(3), 388-400.

Hoshi, E., Shima, K., & Tanji, J. (2000). Neuronal activity in the primate prefrontal cortex in the process of motor selection based on two behavioral rules. *Journal of neurophysiology*, *83*(4), 2355-2373.

Hubel, D. H., & Wiesel, T. N. (1970). The period of susceptibility to the physiological effects of unilateral eye closure in kittens. *The Journal of Physiology*, *206*(2), 419–436.

Hume, D. (1740). *An Abstract of a Treatise of Human Nature.* CUP Archive.

Huttenlocher, P. R. (2009). *Neural plasticity: The effects of environment on the development of the cerebral cortex*. Harvard University Press.

Huttenlocher, P. R., & Dabholkar, A. S. (1997). Regional differences in synaptogenesis in human cerebral cortex. *Journal of Comparative Neurology*, *387*(2), 167–178. https://doi.org/10.1002/(SICI)1096-9861(19971020)387:2<167::AID-CNE1>3.0.CO;2-Z

Ikutani, Y., Kubo, T., Nishida, S., Hata, H., Matsumoto, K., Ikeda, K., & Nishimoto, S. (2021). Expert Programmers Have Fine-Tuned Cortical Representations of Source Code. *eneuro, 8*(1), ENEURO.0405-0420.2020. doi:10.1523/ENEURO.0405-20.2020

Isik, L., Koldewyn, K., Beeler, D., & Kanwisher, N. (2017). Perceiving social interactions in the posterior superior temporal sulcus. *Proceedings of the National Academy of Sciences*, *114*(43), E9145–E9152. https://doi.org/10.1073/pnas.1714471114

Ivanova, A. A., Srikant, S., Sueoka, Y., Kean, H. H., Dhamala, R., O'Reilly, U.-M., . . . Fedorenko, E. (2020). Comprehension of computer code relies primarily on domain-general executive brain regions. *eLife, 9*, e58906. doi:10.7554/eLife.58906

Jorstad, N. L., Close, J., Johansen, N., Yanny, A. M., Barkan, E. R., Travaglini, K. J., ... & Lein, E. S. (2023). Transcriptomic cytoarchitecture reveals principles of human neocortex organization. *Science*, *382*(6667), eadf6812.

Johnson, J. S., & Newport, E. L. (1989). Critical period effects in second language learning: The influence of maturational state on the acquisition of English as a second language. *Cognitive Psychology*, *21*(1), 60–99. https://doi.org/10.1016/0010-0285(89)90003-0

Kadosh, R. C., Kadosh, K. C., Kaas, A., Henik, A., & Goebel, R. (2007). Notation-dependent and-independent representations of numbers in the parietal lobes. Neuron, 53(2), 307-314.

Kahn, D. M., & Krubitzer, L. (2002). Massive cross-modal cortical plasticity and the emergence of a new cortical area in developmentally blind mammals. *Proceedings of the National Academy of Sciences*, *99*(17), 11429-11434.

Kanjlia, S., Feigenson, L., & Bedny, M. (2021). Neural basis of approximate number in congenital blindness. *Cortex*. doi:https://doi.org/10.1016/j.cortex.2021.06.004

Kanjlia, S., Lane, C., Feigenson, L., & Bedny, M. (2016). Absence of visual experience modifies the neural basis of numerical thinking. *Proceedings of the National Academy of Sciences, 113*(40), 11172-11177.

Kanwisher, N., & Yovel, G. (2006). The fusiform face area: A cortical region specialized for the perception of faces. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *361*(1476), 2109–2128. https://doi.org/10.1098/rstb.2006.1934

Kanwisher, N., McDermott, J. & Chun, M. M. (1997) The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J. Neurosci.* **17**, 4302–4311.

Kim, J. S., Aheimer, B., Montané Manrara, V., & Bedny, M. (2021). Shared understanding of color among sighted and blind adults. *Proceedings of the National Academy of Sciences*, *118*(33), e2020192118. https://doi.org/10.1073/pnas.2020192118

Kim, J. S., Elli, G. V., & Bedny, M. (2019). Knowledge of animal appearance among sighted and blind adults. *Proceedings of the National Academy of Sciences*, *116*(23), 11213–11222. https://doi.org/10.1073/pnas.1900952116

Kitayama, S., & Park, J. (2010). Cultural neuroscience of the self: Understanding the social grounding of the brain. *Social cognitive and affective neuroscience*, *5*(2-3), 111-129.

Klima, E. S., & Bellugi, U. (1979). *The signs of language*. Harvard University Press.

Kocab, A., Senghas, A., & Snedeker, J. (2016). The emergence of temporal language in Nicaraguan Sign Language. *Cognition*, *156*, 147-163.

Kosakowski, H. L., Cohen, M. A., Takahashi, A., Keil, B., Kanwisher, N., & Saxe, R. (2022). Selective responses to faces, scenes, and bodies in the ventral visual pathway of infants. *Current Biology*, *32*(2), 265-274.e5. https://doi.org/10.1016/j.cub.2021.10.064

Koster-Hale, J., Bedny, M., & Saxe, R. (2014). Thinking about seeing: Perceptual sources of knowledge are encoded in the theory of mind brain regions of sighted and blind adults. *Cognition*, *133*(1), 65–78. https://doi.org/10.1016/j.cognition.2014.04.006

Krubitzer, L. (1995). The organization of neocortex in mammals: Are species differences really so different? *Trends in Neurosciences*, *18*(9), 408–417. https://doi.org/10.1016/0166-2236(95)93938-T

Krueger, R., Huang, Y., Liu, X., Santander, T., Weimer, W., & Leach, K. (2020). Neurological Divide: An fMRI Study of Prose and Code Writing. Paper presented at the 2020 IEEE/ACM 42nd International Conference on Software Engineering (ICSE).

Kupers, R., Pappens, M., de Noordhout, A. M., Schoenen, J., Ptito, M., & Fumal, A. (2007). rTMS of the occipital cortex abolishes Braille reading and repetition priming in blind subjects. *Neurology*, *68*(9), 691–693. https://doi.org/10.1212/01.wnl.0000255958.60530.11

Kyttälä, M., & Lehto, J. E. (2008). Some factors underlying mathematical performance: The role of visuospatial working memory and non-verbal intelligence. European Journal of Psychology of Education, 23, 77-94

Lai, C. S. L., Fisher, S. E., Hurst, J. A., Vargha-Khadem, F., & Monaco, A. P. (2001). A forkhead-domain gene is mutated in a severe speech and language disorder. *Nature*, *413*(6855), 519–523. https://doi.org/10.1038/35097076

Landau B., & Gleitman L. R. (1985). *Language and experience: Evidence from the blind child.* Cambridge, MA: Harvard University Press

Lane, C., Kanjlia, S., Omaki, A., & Bedny, M. (2015). "Visual" Cortex of Congenitally Blind Adults Responds to Syntactic Movement. *The Journal of Neuroscience*, *35*(37), 12859–12868. https://doi.org/10.1523/JNEUROSCI.1256-15.2015

Larsen, B., & Luna, B. (2018). Adolescence as a neurobiological critical period for the development of higher-order cognition. *Neuroscience & Biobehavioral Reviews*, *94*, 179–195. https://doi.org/10.1016/j.neubiorev.2018.09.005

Legare, C. H. (2017). Cumulative cultural learning: Development and diversity. *Proceedings of the National Academy of Sciences, 114*(30), 7877-7883.

Legare, C. H., & Gelman, S. A. (2008). Bewitchment, biology, or both: The co-existence of natural and supernatural explanatory frameworks across development. *Cognitive Science*, *32*(4), 607-642.

Lenneberg, E. H. (1967). The biological foundations of language. *Hospital Practice*, *2*(12), 59-67.

Leslie, A. M., Gelman, R., & Gallistel, C. R. (2008). The generative basis of natural number concepts. Trends in cognitive sciences, 12(6), 213-218.

Lewis, T. L., & Maurer, D. (2005). Multiple sensitive periods in human visual development: evidence from visually deprived children. *Developmental Psychobiology: The Journal of the International Society for Developmental Psychobiology*, *46*(3), 163-183.

Lewis, L. B., Saenz, M., & Fine, I. (2010). Mechanisms of Cross-Modal Plasticity in Early-Blind Subjects. *Journal of Neurophysiology*, *104*(6), 2995–3008. https://doi.org/10.1152/jn.00983.2009

Libertus, M. E., Feigenson, L., & Halberda, J. (2011). Preschool acuity of the approximate number system correlates with school math ability. Developmental Science, 14(6), 1292-1300. doi:10.1111/j.1467-7687.2011.01080.x

Lillo-Martin, D., & Henner, J. (2021). Acquisition of Sign Languages. *Annual Review of Linguistics*, *7*(1), 395–419. https://doi.org/10.1146/annurev-linguistics-043020-092357

Liu, Y.-F., Kim, J., Wilson, C., & Bedny, M. (2020). Computer code comprehension shares neural resources with formal logical inference in the fronto-parietal network. *eLife, 9*, e59340.

Liu, Y.-F., Wilson, C., & Bedny, M. (2024). Contribution of the language network to the comprehension of Python programming code. *Brain and Language, 251*, 105392.

Locke, J. (1690). *An essay concerning human understanding* (New ed.). London: Ward, Lock, & Co.

Lupyan, G., Rakison, D. H., & McClelland, J. L. (2007). Language is not just for talking: Redundant labels facilitate learning of novel categories. Psychological science, 18(12), 1077-1083.

Lutz, D. J., & Keil, F. C. (2002). Early Understanding of the Division of Cognitive Labor. *Child Development*, *73*(4), 1073–1084. https://doi.org/10.1111/1467-8624.00458

MacSweeney, M., Capek, C. M., Campbell, R., & Woll, B. (2008a). The signing brain: The neurobiology of sign language. *Trends in Cognitive Sciences*, *12*(11), 432–440. https://doi.org/10.1016/j.tics.2008.07.010

MacSweeney, M., Waters, D., Brammer, M. J., Woll, B., & Goswami, U. (2008b). Phonological processing in deaf signers and the impact of age of first language acquisition. *NeuroImage*, *40*(3), 1369–1379.

Mackey, A., Miller Singley, A., & Bunge, S. (2013). Intensive reasoning training alters patterns of brain connectivity at rest. J Neurosci, 33(11), 4796-4803. doi:10.1523/JNEUROSCI.4141-12.2013

Majid, A., Roberts, S. G., Cilissen, L., Emmorey, K., Nicodemus, B., O'grady, L., ... & Levinson, S. C. (2018). Differential coding of perception in the world's languages. Proceedings of the National Academy of Sciences, 115(45), 11369-11376.

Makin, T. R., & Krakauer, J. W. (2023). Against cortical reorganisation. eLife, 12, e84716.

Malik-Moraleda, S., Ayyash, D., Gallée, J., Affourtit, J., Hoffmann, M., Mineroff, Z., Jouravlev, O., & Fedorenko, E. (2022). An investigation across 45 languages and 12 language families reveals a universal language network. *Nature Neuroscience*, *25*(8), 1014–1019. https://doi.org/10.1038/s41593-022-01114-5

Marjieh, R., Sucholutsky, I., van Rijn, P., Jacoby, N., & Griffiths, T. (2023). What language reveals about perception: Distilling psychophysical knowledge from large language models. In *Proceedings of the Annual Meeting of the Cognitive Science Society* (Vol. 45, No. 45).

Marmor, G. S. (1978). Age at onset of blindness and the development of the semantics of color names. *Journal of Experimental Child Psychology*, *25*(2), 267–278. https://doi.org/10.1016/0022-0965(78)90082-6

Marr, D. (1982). Vision: A computational investigation into the human representation and processing of visual information. San Francisco: W. H. Freeman.

Maruyama, M., Pallier, C., Jobert, A., Sigman, M., & Dehaene, S. (2012). The cortical representation of simple mathematical expressions. NeuroImage, 61(4), 1444-1460. doi : https://doi.org/10.1016/j.neuroimage.2012.04.020

Maurer, D., & Werker, J. F. (2014). Perceptual narrowing during infancy: A comparison of language and faces. *Developmental psychobiology*, *56*(2), 154-178.

Mayberry, R. I., & Kluender, R. (2018). Rethinking the critical period for language: New insights into an old question from American Sign Language. *Bilingualism: Language and Cognition*, *21*(5), 886–905. https://doi.org/10.1017/S1366728917000724

McNeill, D. (2012). *How language began: Gesture and speech in human evolution*. Cambridge University Press.

Mead, M. (1928). The Role of the Individual in Samoan Culture. *The Journal of the Royal Anthropological Institute of Great Britain and Ireland*, *58*, 481-495.

Mellor, C. M. (2006). Louis Braille: A touch of genius. National Braille Press

Millar, S. (1984). Is there a "best hand" for braille?. *Cortex*, *20*(1), 75-87.

Millar, S. (2003). *Reading by touch*. Routledge.

Mock, J., Huber, S., Bloechle, J., Bahnmueller, J., Moeller, K., & Klein, E. (2019). Processing symbolic and non-symbolic proportions: Domain-specific numerical and domain-general processes in intraparietal cortex. *Brain Research, 1714*, 133-146.

Monti, M., Parsons, L., & Osherson, D. (2009). The boundaries of language and thought in deductive inference. *Proceedings of the National Academy of Sciences, 106*(30), 12554-12559.

Morishita, H., & Hensch, T. K. (2008). Critical period revisited: Impact on vision. *Current Opinion in Neurobiology*, *18*(1), 101–107. https://doi.org/10.1016/j.conb.2008.05.009

Musz, E., Loiotile, R., Chen, J., & Bedny, M. (2023). Naturalistic Audio-Movies reveal common spatial organization across "visual" cortices of different blind individuals. Cerebral Cortex, 33(1), 1-10.

Musz, E., Loiotile, R., Chen, J., Cusack, R., & Bedny, M. (2022). Naturalistic stimuli reveal a sensitive period in cross modal responses of visual cortex: Evidence from adult-onset blindness. *Neuropsychologia*, *172*, 108277. https://doi.org/10.1016/j.neuropsychologia.2022.108277

Nakai, T., & Sakai, K. L. (2014). Neural Mechanisms Underlying the Computation of Hierarchical Tree Structures in Mathematics. PLoS ONE, 9(11), e111439. doi:10.1371/journal.pone.0111439

Newport, E. L. (1990). Maturational constraints on language learning. *Cognitive science*, *14*(1), 11-28.

Neville, H. J., Coffey, S. A., Lawson, D. S., Fischer, A., Emmorey, K., & Bellugi, U. (1997). Neural systems mediating American Sign Language: Effects of sensory experience and age of acquisition. *Brain and language*, *57*(3), 285-308.

Nieder, A. (2021a). Neuroethology of number sense across the animal kingdom. *Journal of Experimental Biology, 224*(6), jeb218289.

Nieder, A. (2021b). The Evolutionary History of Brains for Numbers. *Trends in Cognitive Sciences, 25*(7), 608-621. doi:10.1016/j.tics.2021.03.012

Nieder, A., & Dehaene, S. (2009). Representation of Number in the Brain. *Annual Review of Neuroscience, 32*(1), 185-208. doi:10.1146/annurev.neuro.051508.135550

Noppeney, U., Friston, K. J., & Price, C. J. (2003). Effects of visual deprivation on the organization of the semantic system. *Brain*, *126*(7), 1620–1627. https://doi.org/10.1093/brain/awg152

Obretenova, S., Halko, M. A., Plow, E. B., Pascual-Leone, A., & Merabet, L. B. (2010). Neuroplasticity associated with tactile language communication in a deaf-blind subject. *Frontiers in human neuroscience*, *3*, 953.

Oomen, M., & Kimmelman, V. (2019). Body-anchored verbs and argument omission in two sign languages. *Glossa: A Journal of General Linguistics*, *4*(1). https://doi.org/10.5334/gjgl.741

Padden, C. A., & Humphries, T. L. (2006). *Inside deaf culture*. Harvard University Press.

Park, H.-J., & Friston, K. (2013). Structural and Functional Brain Networks: From Connections to Cognition. *Science*, *342*(6158), 1238411. https://doi.org/10.1126/science.1238411

Pascual-Leone, A., Amedi, A., Fregni, F., & Merabet, L. B. (2005). The Plastic Human Brain Cortex. *Annual Review of Neuroscience*, *28*(1), 377–401. https://doi.org/10.1146/annurev.neuro.27.070203.144216

Passingham, R. E., Stephan, K. E., & Kötter, R. (2002). The anatomical basis of functional localization in the cortex. *Nature Reviews Neuroscience*, *3*(8), 606-616.

Perniss, P., Pfau, R., & Steinbach, M. (2007). Can't you see the difference? Sources of variation in sign language structure. *Trends in Linguistics Studies and Monographs*, *188*, 1.

Petersen, S. E., & Sporns, O. (2015). Brain Networks and Cognitive Architectures. *Neuron*, *88*(1), 207–219. https://doi.org/10.1016/j.neuron.2015.09.027

Petroni, F., Rocktäschel, T., Lewis, P., Bakhtin, A., Wu, Y., Miller, A. H., & Riedel, S. (2019). *Language Models as Knowledge Bases?* (arXiv:1909.01066). arXiv. http://arxiv.org/abs/1909.01066

Piazza, M., & Eger, E. (2016). Neural foundations and functional specificity of number representations. Neuropsychologia, 83, 257-273. doi:https://doi.org/10.1016/j.neuropsychologia.2015.09.025

Piazza, M., Pinel, P., Le Bihan, D., & Dehaene, S. (2007). A magnitude code common to numerosities and number symbols in human intraparietal cortex. *Neuron, 53*(2), 293-305. doi:https://doi.org/10.1016/j.neuron.2006.11.022

Pinker, S. (2010). The cognitive niche: Coevolution of intelligence, sociality, and language. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 8993–8999. http://dx.doi.org/10.1073/pnas.0914630107

Pizzorusso, T., Medini, P., Berardi, N., Chierzi, S., Fawcett, J. W., & Maffei, L. (2002). Reactivation of Ocular Dominance Plasticity in the Adult Visual Cortex. *Science*, *298*(5596), 1248–1251. https://doi.org/10.1126/science.1072699

Poirier, C., Collignon, O., Scheiber, C., Renier, L., Vanlierde, A., Tranduy, D., Veraart, C., & De Volder, A. G. (2006). Auditory motion perception activates visual motion areas in early blind subjects. *NeuroImage*, *31*(1), 279–285. https://doi.org/10.1016/j.neuroimage.2005.11.036

Pollick, A. S., & de Waal, F. B. M. (2007). Ape gestures and language evolution. *Proceedings of the National Academy of Sciences*, *104*(19), 8184–8189. https://doi.org/10.1073/pnas.0702624104

Prabhakaran, V., Smith, J. A., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. (1997). Neural substrates of fluid reasoning: an fMRI study of neocortical activation during performance of the Raven's Progressive Matrices Test. Cognitive Psychology, 33(1), 43-63.

Prat, C. S., Madhyastha, T. M., Mottarella, M. J., & Kuo, C.-H. (2020). Relating natural language aptitude to individual differences in learning programming languages. *Scientific reports, 10*(1), 3817. doi:10.1038/s41598-020-60661-8

Price, C., Wise, R., & Frackowiak, R. (1996). Demonstrating the Implicit Processing of Visually Presented Words and Pseudowords. *Cerebral Cortex, 6*(1), 62-70. doi:https://doi.org/10.1093/cercor/6.1.62

Purcell, J. J., Napoliello, E. M., & Eden, G. F. (2011). A combined fMRI study of typed spelling and reading. NeuroImage, 55(2), 750-762.

Qin, W., & Yu, C. (2013). Neural Pathways Conveying Novisual Information to the Visual Cortex. Neural plasticity, 2013, 864920. doi:10.1155/2013/864920

Quartz, S. R., & Sejnowski, T. J. (1997). The neural basis of cognitive development: A constructivist manifesto. *Behavioral and Brain Sciences*, *20*(4), 537–556. https://doi.org/10.1017/S0140525X97001581

Raven, J. (1965). Advanced Progressive Matrices. Sets I and II. London: HK Lewis & Co: San Antonio, Texas.

Raz, G., & Saxe, R. (2020). Learning in infancy is active, endogenously motivated, and depends on the prefrontal cortices. Annual Review of Developmental Psychology, 2, 247-268.

Reich, L., Szwed, M., Cohen, L., & Amedi, A. (2011). A Ventral Visual Stream Reading Center Independent of Visual Experience. *Current Biology*, *21*(5), 363–368. https://doi.org/10.1016/j.cub.2011.01.040

Reilly, J. (2006). How faces come to serve grammar: The development of nonmanual morphology in American Sign Language. *Advances in the sign language development of deaf children*, 262-290.

Richardson, H., Koster-Hale, J., Caselli, N., Magid, R., Benedict, R., Olson, H., ... & Saxe, R. (2020). Reduced neural selectivity for mental states in deaf children with delayed exposure to sign language. *Nature communications*, *11*(1), 3246.

Röder, B., Rösler, F., Hennighausen, E., & Näcker, F. (1996). Event-related potentials during auditory and somatosensory discrimination in sighted and blind human subjects. *Cognitive Brain Research*, *4*(2), 77–93. https://doi.org/10.1016/0926-6410(96)00024-9

Röder, B., Stock, O., Bien, S., Neville, H., & Rösler, F. (2002). Speech processing activates visual cortex in congenitally blind humans. *European Journal of Neuroscience*, *16*(5), 930–936. https://doi.org/10.1046/j.1460-9568.2002.02147.x

Saccone, E. J., Tian, M., & Bedny, M. (2024). Developing cortex is functionally pluripotent: Evidence from blindness. Developmental Cognitive Neuroscience, 66, 101360. https://doi.org/10.1016/j.dcn.2024.101360

Sadato, N., Okada, T., Honda, M., & Yonekura, Y. (2002). Critical period for cross-modal plasticity in blind humans: a functional MRI study. NeuroImage, 16(2), 389-400.

Sadato, N., Pascual-Leone, A., Grafman, J., Deiber, M. P., Ibañez, V., & Hallett, M. (1998). Neural networks for Braille reading by the blind. *Brain*, *121*(7), 1213–1229. https://doi.org/10.1093/brain/121.7.1213

Sadato, N., Pascual-Leone, A., Grafman, J., Ibañez, V., Deiber, M.-P., Dold, G., & Hallett, M. (1996). Activation of the primary visual cortex by Braille reading in blind subjects. *Nature*, *380*(6574), 526–528. https://doi.org/10.1038/380526a0

Saxe, R. (2006). Uniquely human social cognition. *Current Opinion in Neurobiology*, *16*(2), 235–239. https://doi.org/10.1016/j.conb.2006.03.001

Saxe, R., & Kanwisher, N. (2003). People thinking about thinking peopleThe role of the temporo-parietal junction in "theory of mind." *NeuroImage*, *19*(4), 1835–1842. https://doi.org/10.1016/S1053-8119(03)00230-1

Saygin, Z. M., Osher, D. E., Norton, E. S., Youssoufian, D. A., Beach, S. D., Feather, J., . . . Kanwisher, N. (2016). Connectivity precedes function in the development of the visual word form area. *Nature Neuroscience, 19*(9), 1250.

Saysani, A., Corballis, M. C., & Corballis, P. M. (2018). Colour envisioned: Concepts of colour in the blind and sighted. *Visual Cognition*, *26*(5), 382–392. https://doi.org/10.1080/13506285.2018.1465148

Schaefer, A., Kong, R., Gordon, E. M., Laumann, T. O., Zuo, X. N., Holmes, A. J., ... & Yeo, B. T. (2018). Local-global parcellation of the human cerebral cortex from intrinsic functional connectivity MRI. *Cerebral cortex*, *28*(9), 3095-3114

Schmandt-Besserat, D., & Erard, M. (2009). Origins and forms of writing Handbook of research on writing (pp. 7-26): Routledge.

Senju, A., Johnson, M. H., & Csibra, G. (2006). The development and neural basis of referential gaze perception. *Social Neuroscience*, *1*(3–4), 220–234. https://doi.org/10.1080/17470910600989797

Shepard, R. N., & Cooper, L. A. (1992). Representation of Colors in the Blind, Color-Blind, and Normally Sighted. *Psychological Science*, *3*(2), 97–104. https://doi.org/10.1111/j.1467-9280.1992.tb00006.x

Sherwood, C. C., & Gómez-Robles, A. (2017). Brain Plasticity and Human Evolution. *Annual Review of Anthropology*, *46*(1), 399–419. https://doi.org/10.1146/annurev-anthro-102215-100009

Shum, J., Fanda, L., Dugan, P., Doyle, W. K., Devinsky, O., & Flinker, A. (2020). Neural correlates of sign language production revealed by electrocorticography. *Neurology*, *95*(21), e2880–e2889. https://doi.org/10.1212/WNL.0000000000010639

Shuman, M., & Kanwisher, N. (2004). Numerical magnitude in the human parietal lobe: Tests of representational generality and domain specificity. *Neuron, 44*(3), 557-569.

Siegmund, J., Kästner, C., Apel, S., Parnin, C., Bethmann, A., Leich, T., . . . Brechmann, A. (2014). Understanding understanding source code with functional magnetic resonance imaging. Paper presented at the Proceedings of the 36th International Conference on Software Engineering.

Spaepen, E., Coppola, M., Spelke, E. S., Carey, S. E., & Goldin-Meadow, S. (2011). Number without a language model. *Proceedings of the National Academy of Sciences, 108*(8), 3163-3168.

Spelke, E. S. (2017). Core Knowledge, Language, and Number. *Language Learning and Development, 13*(2), 147-170. doi:10.1080/15475441.2016.1263572

Spelke, E. S. (2022). *What Babies Know: Core Knowledge and Composition Volume 1*. New York, NY: Oxford University Press.

Sporns, O. (2022). The complex brain: connectivity, dynamics, information. *Trends in cognitive sciences*, *26*(12), 1066-1067.

Srikant, S., Lipkin, B., Ivanova, A. A., Fedorenko, E., & O'Reilly, U.-M. (2022). *Convergent Representations of Computer Programs in Human and Artificial Neural Networks*. Paper presented at the 36th Conference on Neural Information Processing Systems.

Striem-Amit, E., Ovadia-Caro, S., Caramazza, A., Margulies, D. S., Villringer, A., & Amedi, A. (2015). Functional connectivity of visual cortex in the blind follows retinotopic organization principles. *Brain*, *138*(6), 1679–1695. https://doi.org/10.1093/brain/awv083

Striem-Amit, E., Wang, X., Bi, Y., & Caramazza, A. (2018). Neural representation of visual concepts in people born blind. *Nature Communications*, *9*(1), 5250. https://doi.org/10.1038/s41467-018-07574-3

Szwed, M., Dehaene, S., Kleinschmidt, A., Eger, E., Valabrègue, R., Amadon, A., & Cohen, L. (2011). Specialization for written words over objects in the visual cortex. *NeuroImage, 56*(1), 330-344.

Tennie, C., Call, J., & Tomasello, M. (2009). Ratcheting up the ratchet: On the evolution of cumulative culture. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1528), 2405–2415. https://doi.org/10.1098/rstb.2009.0052

Terrace, H. S., Petitto, L. A., Sanders, R. J., & Bever, T. G. (1979). Can an Ape Create a Sentence? *Science*, *206*(4421), 891–902. https://doi.org/10.1126/science.504995

Thompson-Schill, S. L., D'Esposito, M., Aguirre, G. K., & Farah, M. J. (1997). Role of left inferior prefrontal cortex in retrieval of semantic knowledge: a reevaluation. Proceedings of the National Academy of Sciences, 94(26), 14792-14797.

Thompson-Schill, S. L., Ramscar, M., & Chrysikou, E. G. (2009). Cognition without control: When a little frontal lobe goes a long way. Current Directions in Psychological Science, 18(5), 259-263.

Tian, M., Saccone, E. J., Kim, J. S., Kanjlia, S., & Bedny, M. (2023). Sensory modality and spoken language shape reading network in blind readers of Braille. *Cerebral Cortex*, *33*(6), 2426–2440. https://doi.org/10.1093/cercor/bhac216

Tian, M., Xiao, X., Hu, H., Cusack, R., & Bedny, M. (2024). Visual experience shapes functional connectivity between occipital and non-visual networks. *eLife*, *13*. https://doi.org/10.7554/eLife.93067.1

Tomasello, M. (1999). The Human Adaptation for Culture. *Annual Review of Anthropology*, *28*(1), 509–529. https://doi.org/10.1146/annurev.anthro.28.1.509

Tomasello, M. (2010). *Origins of human communication*. MIT press.

Tooby, J., & Cosmides, L. (1992). The psychological foundations of culture. *The adapted mind: Evolutionary psychology and the generation of culture*, *19*(1), 1-136.

Tooby, J., & DeVore, I. (1987). The reconstruction of hominid behavioral evolution through strategic modeling. In W. G. Kinzey (Ed.), *The evolution of human behavior: Primate models*. Albany, NY: SUNY Press.

Tsapkini, K., & Rapp, B. (2010). The orthography-specific functions of the left fusiform gyrus: Evidence of modality and category specificity. Cortex, 46(2), 185-205.

Tudusciuc, O., & Nieder, A. (2009). Contributions of primate prefrontal and posterior parietal cortices to length and numerosity representation. Journal of neurophysiology, 101(6), 2984-2994. doi:10.1152/jn.90713.2008

Van Den Heuvel, M. P., & Sporns, O. (2011). Rich-Club Organization of the Human Connectome. *The Journal of Neuroscience*, *31*(44), 15775–15786. https://doi.org/10.1523/JNEUROSCI.3539-11.2011

Vendrell, P., Junqué, C., Pujol, J., Jurado, M. A., Molet, J., & Grafman, J. (1995). The role of prefrontal regions in the Stroop task. *Neuropsychologia*, *33*(3), 341-352.

Vinckier, F., Dehaene, S., Jobert, A., Dubus, J. P., Sigman, M., & Cohen, L. (2007). Hierarchical Coding of Letter Strings in the Ventral Stream: Dissecting the Inner Organization of the Visual Word-Form System. *Neuron, 55*(1), 143-156. doi:https://doi.org/10.1016/j.neuron.2007.05.031

Von Melchner, L., Pallas, S. L., & Sur, M. (2000). Visual behaviour mediated by retinal projections directed to the auditory pathway. Nature, 404(6780), 871-876.

Wallis, J. D., Anderson, K. C., & Miller, E. K. (2001). Single neurons in prefrontal cortex encode abstract rules. *Nature*, *411*(6840), 953-956.

Wanet-Defalque, M.-C., Veraart, C., De Volder, A., Metz, R., Michel, C., Dooms, G., & Goffinet, A. (1988). High metabolic activity in the visual cortex of early blind human subjects. *Brain Research*, *446*(2), 369–373. https://doi.org/10.1016/0006-8993(88)90896-7

Wang, J., Halberda, J., & Feigenson, L. (2017). Approximate number sense correlates with math performance in gifted adolescents. Acta psychologica, 176, 78-84. doi:https://doi.org/10.1016/j.actpsy.2017.03.014

Wang, X., Men, W., Gao, J., Caramazza, A., & Bi, Y. (2020). Two Forms of Knowledge Representations in the Human Brain. *Neuron*, *107*(2), 383-393.e5. https://doi.org/10.1016/j.neuron.2020.04.010

Weiner, K. S., Barnett, M. A., Lorenz, S., Caspers, J., Stigliani, A., Amunts, K., ... & Grill-Spector, K. (2017). The cytoarchitecture of domain-specific regions in human high-level visual cortex. Cerebral cortex, 27(1), 146-161.

Wellman, H. M., Carey, S., Gleitman, L., Newport, E. L., & Spelke, E. S. (1990). *The child's theory of mind*. The MIT Press.

Werchan, D. M., Collins, A. G., Frank, M. J., & Amso, D. (2016). Role of prefrontal cortex in learning and generalizing hierarchical rules in 8-month-old infants. Journal of Neuroscience, 36(40), 10314-10322.

Werker, J. F., & Hensch, T. K. (2015). Critical Periods in Speech Perception: New Directions. Annual Review of Psychology, 66(1), 173–196. https://doi.org/10.1146/annurev-psych-010814-015104

Wolbers, T., Zahorik, P., & Giudice, N. A. (2011). Decoding the direction of auditory motion in blind humans. *NeuroImage*, *56*(2), 681–687. https://doi.org/10.1016/j.neuroimage.2010.04.266

Woll, B. (2018). The consequences of very late exposure to BSL as an L1. *Bilingualism: Language and Cognition*, *21*(5), 936–937. https://doi.org/10.1017/S1366728918000238

Woll, B., Sutton-Spence, R., & Elton, F. (2001). Multilingualism: The global approach to sign languages. *The sociolinguistics of sign languages*, *8*, 32.

Woodward, A. L. (1998). Infants selectively encode the goal object of an actor's reach. Cognition, 69(1), 1-34.

Woolgar, A., Jackson, J., & Duncan, J. (2016). Coding of visual, auditory, rule, and response information in the brain: 10 years of multivoxel pattern analysis. *Journal of cognitive neuroscience*, *28*(10), 1433-1454.

Wright, S., Matlen, B., Baym, C., Ferrer, E., & Bunge, S. (2008). Neural correlates of fluid reasoning in children and adults. *Frontiers in Human Neuroscience, 2*(8). doi:10.3389/neuro.09.008.2007

Xu, M., Baldauf, D., Chang, C. Q., Desimone, R., & Tan, L. H. (2017). Distinct distributed patterns of neural activity are associated with two languages in the bilingual brain. *Science Advances*, *3*(7), e1603309. https://doi.org/10.1126/sciadv.1603309

Xu, S., Li, Y., & Liu, J. (2021). The Neural Correlates of Computational Thinking: Collaboration of Distinct Cognitive Components Revealed by fMRI. *Cerebral Cortex*. doi:10.1093/cercor/bhab182

Xu, F., Spelke, E. S., & Goddard, S. (2005). Number sense in human infants. Developmental Science, 8(1), 88-101.

Yang, C. (2013). Ontogeny and phylogeny of language. *Proceedings of the National Academy of Sciences*, *110*(16), 6324–6327. https://doi.org/10.1073/pnas.1216803110

Yaple, Z. A., Stevens, W. D., & Arsalidou, M. (2019). Meta-analyses of the n-back working memory task: fMRI evidence of age-related changes in prefrontal cortex involvement across the adult lifespan. *NeuroImage*, *196*, 16-31.

Yeung, M. S. Y., Zdunek, S., Bergmann, O., Bernard, S., Salehpour, M., Alkass, K., Perl, S., Tisdale, J., Possnert, G., Brundin, L., Druid, H., & Frisén, J. (2014). Dynamics of Oligodendrocyte Generation and Myelination in the Human Brain. *Cell*, *159*(4), 766–774. https://doi.org/10.1016/j.cell.2014.10.011

Zimmermann, M., Cusack, R., Bedny, M., & Szwed, M. (in press). Auditory areas are recruited for naturalistic visual meaning in early deaf people. *Nature Communications*.