ANNUAL REVIEWS

Annual Review of Developmental Psychology

Built to Adapt: Mechanisms of Cognitive Flexibility in the Human Brain

Miriam Hauptman, Yun-Fei Liu, and Marina Bedny

Department of Psychological and Brain Sciences, Johns Hopkins University, Baltimore, Maryland, USA; email: mhauptm1@jhu.edu, yliu291@jhu.edu, marina.bedny@jhu.edu

Annu. Rev. Dev. Psychol. 2024. 6:133–62

First published as a Review in Advance on September 24, 2024

The *Annual Review of Developmental Psychology* is online at devpsych.annualreviews.org

https://doi.org/10.1146/annurev-devpsych-120621-042108

Keywords

plasticity, blindness, reuse, cultural recycling, language, expertise

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? Here 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 (frontoparietal 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.

Contents

1. INTRODUCTION

Anthropologists have long pointed out that humans occupy a wide range of habitats and exhibit diverse knowledge and behavior (e.g., Benedict 1935, Boas 1896, Henrich & McElreath 2003, Mead 1928, Tooby & DeVore 1987). 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. 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 (Boyd et al. 2011, Legare 2017, Tomasello 1999, Tooby & Cosmides 1992, Tooby & DeVore 1987). Humans have been described as generalist specialists because of our ability to develop specialized behaviors to meet the demands of highly variable environments (Roberts & Stewart 2018). Archeological evidence suggests that this unparalleled adaptability contributed to the survival of *Homo sapiens* as a species (Potts 1998, Zeller et al. 2023). Here we discuss the neural mechanisms that enable this adaptability.

Drawing upon psychological and cognitive neuroscience studies of variation in human experience, we propose a flexible specialization account. Our species' unusual adaptability is supported by a combination of (*a*) evolutionarily prepared neural systems that enable distinctively human flexible learning and (*b*) the expanded capacity for functional plasticity of the human brain that enables it to support cognitive abilities not selected for by evolution.

Human brains have evolved domain-specific and domain-general systems that enable flexible learning. Language is an example of a distinctively human domain-specific system that enables flexible learning through social communication. Domain-general reasoning systems in frontoparietal cortices are likewise elaborated in humans and evolutionarily prepared to support novel problem solving and flexible learning (Badre & Nee 2018, Duncan 2010, Woolgar et al. 2016). As we discuss below, these systems are themselves plastic, but are nevertheless evolutionarily prepared to enable specific cognitive capacities.

On the other hand, human adaptability is made possible by the more open-ended functional flexibility of neural wetware. Our brains are built to go beyond built-in cognitive capacities through functional plasticity. As David Marr (1982) observed, mental software is partly independent from the hardware in which it is implemented. 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 this open-ended 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 one another. 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 the respective contributions of each 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.

This 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, sight) (Campbell & Bergelson 2022, Kim et al. 2019, Landau & Gleitman 1985). 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 (Carrigan & Coppola 2017, Goldin-Meadow 2005, 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[1] are therefore not merely a loss of 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.

The current account draws inspiration from several prior proposals. One such proposal is Dehaene & Cohen's (2007) cultural recycling of cortical maps. Our account shares with this proposal

---

[1] Uppercase "Deaf" is used to describe people who identify as culturally Deaf, while lowercase "deaf" is used to describe audiological status (Woodward 1972). We use lowercase deaf throughout this article to refer to people who may or may not identify as culturally Deaf.

the idea that the modification of innate domain-specific circuitry is an important mechanism of cultural adaptation. We do not discuss this mechanism in detail in this 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 this article, 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., Heyes 2018, Quartz & Sejnowski 1997). 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 hardcoded 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 that 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 (Isik et al. 2017, Kanwisher et al. 1997). 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, that is, that there are no immutable cognitive workings. Cognitive flexibility and specialization of cortical circuits coexist.

The remainder of the article is organized as follows. First, we describe five proposed mechanisms of adaptation (Section 2; see also **Figure 1**). 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 (Section 2.1), and frontoparietal reasoning circuits are an example of a domain-general mechanism (Section 2.2). The last three mechanisms are properties of the human brain that enable functional plasticity: heightened plasticity during

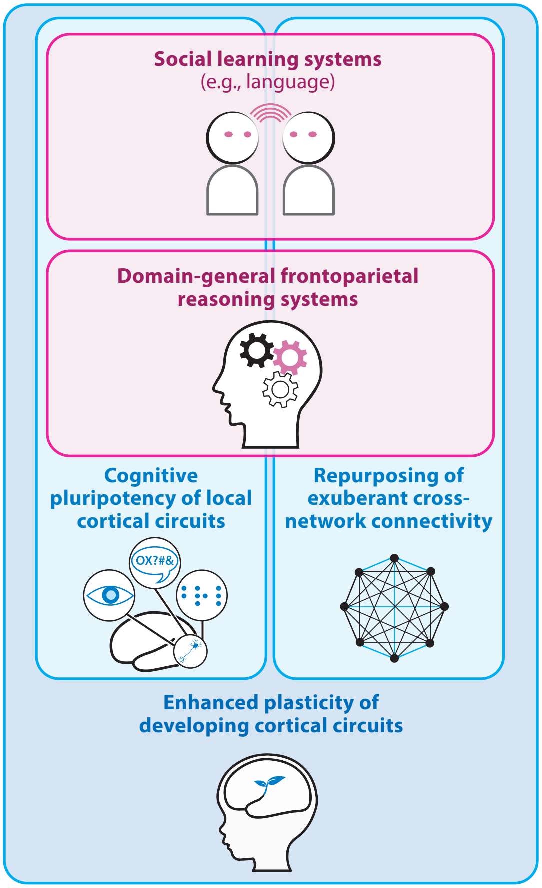

Figure 1

Mechanisms of adaptation according to the flexible specialization account. The mechanisms shown in pink are evolutionarily prepared neurocognitive systems that enable uniquely human flexible learning. The mechanisms shown in blue are general mechanisms of functional plasticity.

development (Section 2.3), cognitive pluripotency of cortical circuits (Section 2.4), and exuberant cross-system connectivity (Section 2.5). Next, we review empirical examples of adaptation that provide evidence for these mechanisms (Section 3): blindness (Section 3.1), language acquisition (Section 3.2), and the acquisition of cultural symbol systems (reading, math, and programming) (Section 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., Carey 2009, Gopnik & Wellman 1992, Gweon 2021, Saxe 2006, Spelke 2022, Tomasello 1999, Wellman et al. 1990). Our ability and desire to learn from others allow 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 (Tennie et al. 2009, Tomasello 1999). 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 (Gopnik & Wellman 1992, Saxe & Kanwisher 2003, Woodward 1998). Human social learning also critically depends on language, which enables efficient communication (Gelman 2009, Lupyan et al. 2007, Pinker 2010, Tooby & DeVore 1987). In this article, 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., Bellugi et al. 1989, Broca 1861, Chomsky 1965, 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 enable 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, Friedrich & Friederici 2013, Liu et al. 2024, Maruyama et al. 2012, Price et al. 1996).

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 (Gelman 2009, Pinker 2010, Tooby & DeVore 1987). For example, children use language to learn about mental states, the causes of illnesses, religious beliefs, the life cycle, and moral norms (e.g., Gelman 2009, Harris & Koenig 2006, Legare & Gelman 2008, Spelke 2022). 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 Frontoparietal Reasoning Systems

In addition to specialized domain-specific systems, human adaptation depends on evolutionarily prepared domain-general reasoning abilities that are supported by frontoparietal 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 such as 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) (Thompson-Schill et al. 1997, Vendrell et al. 1995, Yaple et al. 2019).

In human brains, frontoparietal 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, Coetzee & Monti 2018, Danker & Anderson 2007, Woolgar et al. 2016). Moreover, in nonhuman primates, prefrontal neurons encode conditionals, such as "if cue A, then respond to a matching stimulus; if cue B, then respond to a nonmatch" (Hoshi et al. 2000, Wallis et al. 2001), as well as numerical rules such as greater than versus 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 frontoparietal 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 suggest 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 (Section 3.1.2), congenital sensory loss has much larger effects on the function of sensory cortices compared with acquired sensory loss (e.g., Burton 2003, Cohen et al. 1999, Musz et al. 2022, Sadato et al. 2002). 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 (Crair et al. 1998; Hensch 2004, 2005; Hubel & Wiesel 1970). 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 with other primates, providing a longer opportunity for experience to influence brain function (Hartley 2022, Sherwood & Gómez-Robles 2017). Neurodevelopmental processes such as synaptogenesis, synaptic pruning, and myelination unfold throughout childhood, with many higher cognitive regions reaching full maturity only after adolescence (Gogtay et al. 2004, Huttenlocher 2009, Huttenlocher & Dabholkar 1997, Larsen & Luna 2018, Yeung et al. 2014). The extended neural development of higher cognitive systems and their expansiveness in the human brain enhance 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 interneuronal connectivity patterns (Jorstad et al. 2023, Passingham et al. 2002). There is also covariation between these cytoarchitectural features and cortical functions (e.g., some visual areas have a characteristic cytoarchitecture; 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., Bedny 2017, Collignon et al. 2009, Kahn & Krubitzer 2002). Local circuits have the 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 a recent review, see Saccone et al. 2024). Cortical circuits thought to have evolved for low-level vision (e.g., V1/BA17) participate in nonvisual functions in blindness (e.g., language)

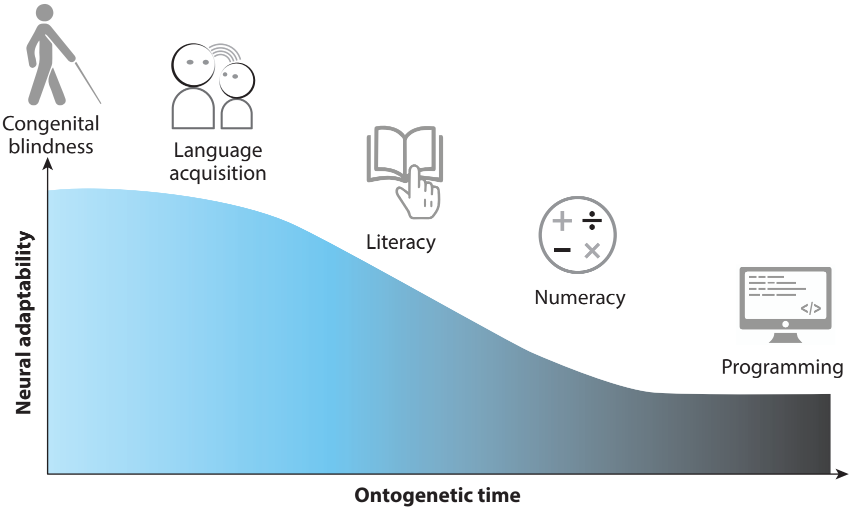

Figure 2

Experiential variation and neural adaptability. The figure shows 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.

(Bedny et al. 2011, Röder et al. 2002, Sadato et al. 1996). 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 frontotemporal language networks of children acquiring different languages is an example of more subtle functional plasticity (Emmorey 2021, MacSweeney et al. 2008a, 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 this 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) (Fedorenko et al. 2011, Kanwisher et al. 1997). 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 (Friederici 2009, Petersen & Sporns 2015, Park & Friston 2013, Schaefer et al. 2018). Cross-network connectivity is particularly pronounced among higher cognitive circuits (e.g., "rich-club" hubs) and between higher cognitive and sensory systems (Bullmore & Sporns 2012, van den Heuvel & Sporns 2011). 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 this article makes use of cross-network connectivity. For example, visual areas take on nonvisual functions via connectivity between the visual system and nonvisual networks in blindness. Our capacity to acquire and process spoken, visual-manual (sign), and tactile (braille) language 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(s) supported by a cross-system connection in a given case of adaptation may be related to the function(s) 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 (Burton et al. 2014, Deen et al. 2015, Striem-Amit 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 (Bouhali et al. 2014, Saygin et al. 2016). How a connection is reused is determined by what we refer to as its cognitive affordance, that is, 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 (Epstein et al. 2007, Kanwisher & Yovel 2006, Senju & Csibra 2008). 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 to any other sensory system (Grill-Spector & Malach 2004). Many visual neural structures are evolutionarily ancient, that is, they are shared across most mammals (Espinosa & Stryker 2012, Krubitzer 1995). The human brain is therefore built to see.

Nevertheless, humans who are born blind carry out seemingly visual tasks using nonvisual information. Blind and sighted children develop spatial representations, language, and social cognition in a remarkably similar manner (e.g., Campbell et al. 2024, Landau & Gleitman 1985). Blind individuals adapt to sensory loss in uniquely human ways. People who are blind invent, teach, and use nonvisual 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., Bedny et al. 2019, Shepard & Cooper 1992). Neural structures that enable vision in sighted people are repurposed for nonvisual functions in blindness, including uniquely human functions such as language and cultural inventions such as braille reading and mathematics (e.g., Bedny et al. 2011, Kanjlia et al. 2016, Röder et al. 2002, Sadato et al. 1996). In this section, 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 knowledge 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 such as Locke and Hume, who emphasized the importance of sensory experience in learning, argued that visual phenomena are inaccessible to blind people (e.g., Hume 1740, Locke 1690). Such intuitions persist in modern-day psychology, education, and neuroscience (e.g., Barsalou 1999, Bigelow 1987, Dunlea 1989, Gallese & Lakoff 2005). 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 comparable 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 versus glance) and light-emission events (e.g., sparkle versus flash) (Bedny et al. 2019, Marmor 1978, Saysani et al. 2018, Shepard & Cooper 1992).

Neuroscientific studies suggest that thinking about visual categories engages similar neural systems across blind and sighted people (Bedny et al. 2012, Hauptman et al. 2023, Koster-Hale et al. 2014, Noppeney et al. 2003, Striem-Amit et al. 2018). For example, blind and sighted adults activate overlapping neural circuits when thinking about colors and visual weather events such as a 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 an 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 LLMs. 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, Gurnee & Tegmark 2024, Marjieh et al. 2023). However, humans and 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, such as 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 noncanonical 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 nonvisual functions, including braille reading, auditory localization, and decision-making in auditory and tactile tasks (e.g., Röder et al. 1996, Sadato et al. 1996, Wanet-Defalque et al. 1988). Responses to nonvisual tasks are observed throughout the visual hierarchy, from high-level visual areas in the dorsal and ventral streams to primary visual cortex (e.g., Burton 2003, Burton et al. 2003, Röder et al. 2002). Analogous functional changes are also observed in 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 (Zimmermann et al. 2024).

The precise function of visual areas in people who are born blind remains debated. Responses to nonvisual stimuli in visual cortices of blind people have 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 (Bedny et al. 2010, Poirier et al. 2006, 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 (Abboud & Cohen 2019; Bedny et al. 2011; Crollen et al. 2019; Kanjlia et al. 2016, 2021; Röder et al. 2002; Sadato et al. 1996, 1998). Activity in visual cortices of blind people is sensitive to abstract cognitive information, including the grammatical complexity of sentences and their meanings (Bedny et al. 2011, Lane et al. 2015, Röder et al. 2002). 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 nonvisual tasks, including braille reading and verb generation (Amedi et al. 2004, Cohen et al. 1997, 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 nonvisual 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 nonvisual information in visual cortices are found in people who are born blind (Bedny et al. 2012, Burton 2003, Cohen et al. 1999, Musz et al. 2022, Sadato et al. 2002). This observation suggests that functional change in visual cortex is dependent on mechanisms of heightened plasticity in the developing brain (Crair et al. 1998; Hensch 2004, 2005).

Why and how do visual networks take on higher cognitive functions? Exuberant connectivity appears to be a key part of the answer (Bedny 2017, Lewis et al. 2010). Visual areas are connected with language networks in sighted and blind people (Bedny et al. 2011, Saygin et al. 2016). The visual system of sighted humans also receives rich top-down connectivity from frontoparietal 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 frontoparietal 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 (Abboud & Cohen 2019; Bedny et al. 2011; Kanjlia et al. 2016, 2021). Elements of this blind functional connectivity profile are present in sighted infants (Tian et al. 2024), 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 nonvisual 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 nonverbal 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 (Gelman 2009, Pinker 2010, Tooby & DeVore 1987). It is also a key example of how evolutionary preparedness coexists with flexibility. The language system exhibits multiple signatures of innate specification. These include (*a*) commonalities in language use across humans, (*b*) resilient acquisition in childhood without explicit instruction, and (*c*) dedicated neurobiological machinery. Languages that are not historically linked share numerous commonalities, such as use of word order (e.g., subject–verb–object in English, Hmong Njua), grammatical gender (e.g., Dyirbal, German), and lexical tones (e.g., Mandarin, Cherokee) (Comrie 1999, Dryer 2007). Language acquisition unfolds effortlessly and follows a similar trajectory across children growing up in different linguistic communities (Clark & Casillas 2015, Gleitman & Newport 1995). 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

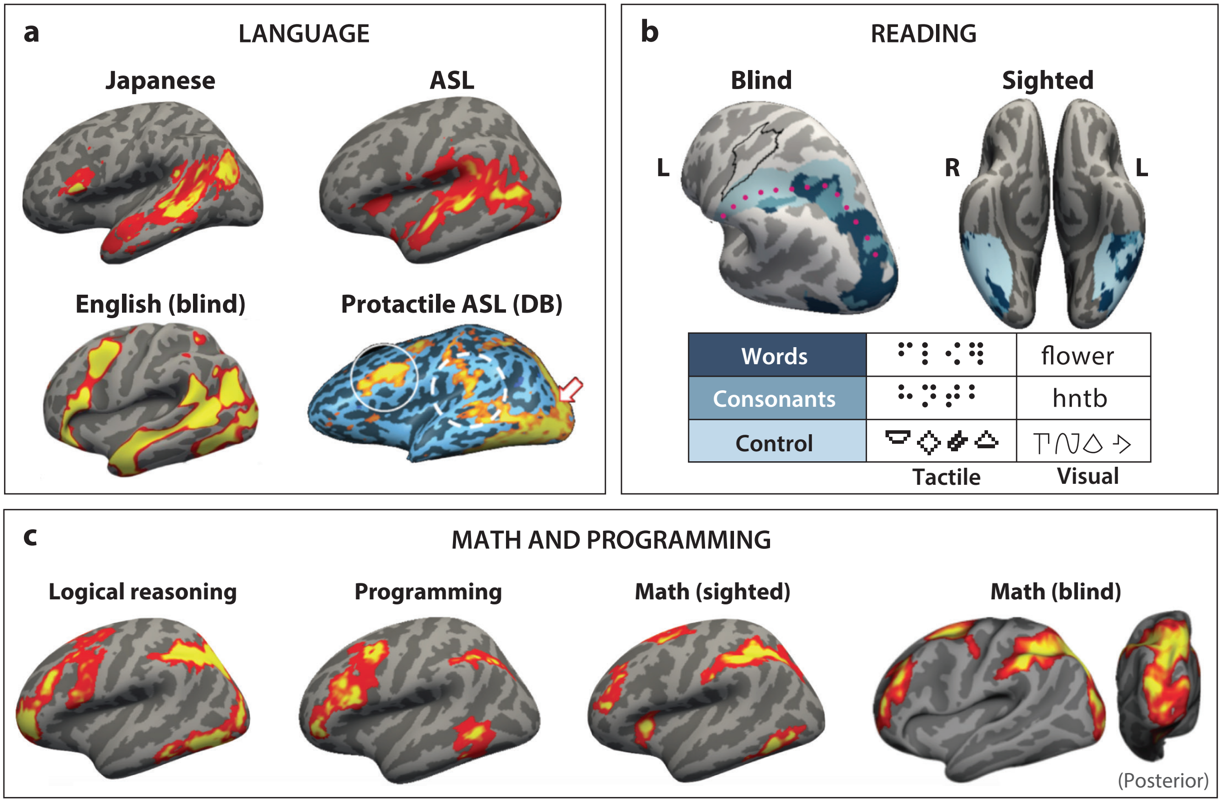

Figure 3

Examples of neural stability and adaptability across cognitive systems. The symbol > is used to indicate a univariate contrast between experimental conditions. (*a*) Commonalities and differences in language network. Blindness leads to the additional recruitment of visual circuits for language processing (*bottom row*). (*a*, *top left*) Japanese sentences > nonwords in one participant (Malik-Moraleda et al. 2022). (*a*, *top right*) American Sign Language (ASL) > matched action videos in a deaf participant (unpublished data). (*a*, *bottom left*) Spoken English sentences > nonwords in a congenitally blind participant (Lane et al. 2015). (*a*, *bottom right*) Protactile words > nonwords in a DeafBlind (DB) participant (Obretenova et al. 2010). (*b*) Distinct reading streams in visual and braille reading (Tian et al. 2023). (*c*) Similar neural responses to logical reasoning (Liu et al. 2020), programming (Liu et al. 2020), and math (blind and sighted) (Kanjlia et al. 2016, Liu et al. 2020). Blindness leads to the additional recruitment of visual circuits for math processing. Contrasts are presented from left to right: logical reasoning > language, programming > working memory control, and math equations > sentences. The bottom right image in panel *a* adapted with permission from Obretenova et al. (2010). Panel *b* adapted with permission from Tian et al. (2023). The programming image in panel *c* adapted with permission from Liu et al. (2020).

our closest living ancestors (chimpanzees) language have proven unsuccessful (Terrace et al. 1979, Yang 2013). A network of left-lateralized frontotemporal brain regions exhibits high selectivity for language compared with other cognitive functions (Bates et al. 1991, Fedorenko et al. 2011, Hickok et al. 1996, Malik-Moraleda et al. 2022) (**Figure 3*a***). Several genes related to human language abilities have also been identified, including *FOXP2*, which is thought to have been the target of recent selection (Enard et al. 2002, Lai et al. 2001). 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., Chandrasekaran et al. 2007, Xu et al. 2017).

Critically, optimal language learning depends on early language experience (Gleitman & Newport 1995, Hartshorne et al. 2018, Lenneberg 1967). 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, MacSweeney et al. 2008b, Newport 1990). 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 (Cheng et al. 2019, Ferjan-Ramirez et al. 2014, Woll 2018). 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 the 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 each have a distinct phonology, morphology, and syntax (Klima & Bellugi 1979, Perniss et al. 2007). 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, Oomen & Kimmelman 2019, Reilly 2006).

Sign language comprehension and production activate canonical left-lateralized frontotemporal language regions, including the left inferior frontal and middle temporal gyri (Campbell et al. 2007, Emmorey 2021, MacSweeney et al. 2008a, Neville et al. 1997, Richardson et al. 2020) (**Figure 3*a***). 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 with respect to cultural symbol systems (Section 3.3) and therefore only briefly mention it here as it relates to the multimodality 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 (Arbib et al. 2008, Corballis 1999, McNeill 2012, Pollick & de Waal 2007, Tomasello 2010). 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 frontotemporal regions plus visual cortex during PT comprehension (Obretenova et al. 2010) (**Figure 3*a***). 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 occipitotemporal cortex (vOTC) that participate in visual reading (e.g., Reich et al. 2011, Sadato et al. 1996). 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 3*b***).

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 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 (de Voogt 2021, Schmandt-Besserat & Erard 2008). 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 frontotemporal 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 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 nonlinguistic 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 3*b***). 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 (Bouhali et al. 2014, Saygin et al. 2016). 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 preliterate children and illiterate adults), the anatomical location of the VWFA is involved in visual object recognition (Dehaene-Lambertz et al. 2018, Saygin et al. 2016). 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" (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 with speakers of languages with exact number words (Boni et al. 2022, Frank et al. 2008, Gordon 2004, Spaepen et al. 2011). This evidence suggests that linguistic and cultural experience influence numerical cognition.

Although language contributes to the development of exact numerical cognition, the frontotemporal 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 of numerical cognition is the so-called approximate number system, which is implemented in frontoparietal 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 (Feigenson et al. 2004, Xu et al. 2005). 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 frontoparietal 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., four versus eight) can be decoded from patterns of neural activity in the human intraparietal sulcus (IPS) (Damarla & Just 2013, Eger et al. 2009, Kanjlia et al. 2021, Piazza & Eger 2016). In nonhuman 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). Frontoparietal 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, Leslie et al. 2008, Spelke 2017). 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 frontoparietal cortex neighbor one other but are not the same: Classifiers trained to distinguish neural patterns elicited during approximate number tasks (e.g., 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, frontoparietal 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 frontoparietal networks encode abstract hierarchical rule sets (Bengtsson et al. 2009, Bunge et al. 2003, 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 nonverbal reasoning tasks such as Raven's Advanced Progressive Matrices (Fedorenko et al. 2013, Prabhakaran et al. 1997, Raven 1965, Xu et al. 2021). Individual differences in core functions of domain-general frontoparietal circuits, including executive control, working memory, and nonverbal 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). Frontoparietal 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 frontoparietal reasoning networks in cultural symbol systems. Like mathematics, programming involves the manipulation of abstract symbols and the use of logical rules (e.g., IF conditionals 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 frontoparietal reasoning networks.

Comprehension of programming code (including C, Python, Java, and Scratch) engages a domain-general frontoparietal reasoning network (Floyd et al. 2017, Ikutani et al. 2021, Ivanova et al. 2020, Liu et al. 2020). Programming skills are predicted by deductive reasoning abilities and working memory capacity, but not linguistic skills (for a review, see Farghaly & El-Kafrawy 2021). Neural responses to code comprehension in individual brains overlap with frontoparietal 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 frontoparietal 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 frontoparietal 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 frontoparietal reasoning network's propensity for representing rules and contingencies is recycled by the cultural phenomenon of programming (e.g., Bengtsson et al. 2009, Bunge et al. 2003, 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 frontoparietal circuits or capacities that themselves are acquired earlier in childhood through learning remains to be fully understood. Frontoparietal networks are engaged in logical reasoning in children as young as 6 years of age (Crone et al. 2009, Wright et al. 2008). As mentioned above, frontoparietal networks continue to mature anatomically and functionally for an extended period of time (Hartley et al. 2021, Thompson-Schill et al. 2009, Werchan et al. 2016). Little is known about the function of these systems in early infancy. There is some evidence that frontoparietal systems are engaged in simple rule-learning in 8-month-old infants (Raz & Saxe 2020, Werchan et al. 2016). Recent behavioral evidence suggests that preverbal infants engage in basic forms of logical reasoning, such as disjunctive syllogism deduction (Cesana-Arlotti et al. 2018, 2020; Feiman et al. 2022). Emerging imaging studies with infants further suggest that despite their slow maturation, frontoparietal 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 one another 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 depend 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 such as "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.

4. 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., Cetron et al. 2020, Mackey et al. 2013). 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, for example, that 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 this article 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 review apply broadly, that is, 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 review, such as cognitive pluripotency and exuberant connectivity, were specifically selected for in the human lineage because they enable flexible adaptation. Recent archeological evidence suggests that *Homo sapiens* are distinctive as a species in their affinity for environmental diversity (Roberts & Stewart 2018, Zeller et al. 2023). Some prior work suggests that human brains are more plastic than those of other primates (Sherwood & Gómez-Robles 2017). Future studies comparing adaptability across species could provide insight into such questions.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

This work was supported by grants from the National Science Foundation (BCS-2318685) and the National Institutes of Health/National Eye Institute (R01 EY027352-01). The authors thank Rebecca Saxe for her thoughtful comments on an earlier draft of this article and Akshi and Saima Malik-Moraleda for contributing their data to **Figure 3**. We would also like to thank Lindsay Yazzolino for her invaluable insights on visual knowledge in blindness over the past 15 years. We thank the blind community and the National Federation of the Blind for their support of cognitive and neuroscience research. The blind community's generous willingness to give their time and share their lived experiences enables scientific progress.

LITERATURE CITED

Abboud S, Cohen L. 2019. Distinctive interaction between cognitive networks and the visual cortex in early blind individuals. *Cereb. Cortex* 29(11):4725–42

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 [cx.CV]

Almeida D, Poeppel D, Corina D. 2016. The processing of biologically plausible and implausible forms in American Sign Language: evidence for perceptual tuning. *Lang. Cogn. Neurosci.* 31(3):361–74

Amalric M, Dehaene S. 2018. Cortical circuits for mathematical knowledge: evidence for a major subdivision within the brain's semantic networks. *Philos. Trans. R. Soc. B Biol. Sci.* 373(1740):20160515

Amalric M, Dehaene S. 2019. A distinct cortical network for mathematical knowledge in the human brain. *NeuroImage* 189:19–31

Amalric M, Denghien I, Dehaene S. 2018. On the role of visual experience in mathematical development: evidence from blind mathematicians. *Dev. Cogn. Neurosci.* 30:314–23

Amedi A, Floel A, Knecht S, Zohary E, Cohen LG. 2004. Transcranial magnetic stimulation of the occipital pole interferes with verbal processing in blind subjects. *Nat. Neurosci.* 7(11):1266–70

Amedi A, Raz N, Pianka P, Malach R, Zohary E. 2003. Early 'visual' cortex activation correlates with superior verbal memory performance in the blind. *Nat. Neurosci.* 6(7):758–66

Amunts K, Zilles K. 2015. Architectonic mapping of the human brain beyond Brodmann. *Neuron* 88(6):1086–107

Anderson JR, Lee HS, Fincham JM. 2014. Discovering the structure of mathematical problem solving. *NeuroImage* 97:163–77

Anderson ML. 2010. Neural reuse: a fundamental organizational principle of the brain. *Behav. Brain Sci.* 33(4):245–66

Ansari D. 2008. Effects of development and enculturation on number representation in the brain. *Nat. Rev. Neurosci.* 9(4):278–91

Arbib MA, Liebal K, Pika S. 2008. Primate vocalization, gesture, and the evolution of human language. *Curr. Anthropol.* 49(6):1053–76

Badre D, Kayser AS, D'Esposito M. 2010. Frontal cortex and the discovery of abstract action rules. *Neuron* 66(2):315–26

Badre D, Nee DE. 2018. Frontal cortex and the hierarchical control of behavior. *Trends Cogn. Sci.* 22(2):170–88

Baluch F, Itti L. 2011. Mechanisms of top-down attention. *Trends Neurosci.* 34(4):210–24

Barnes E. 2016. *The Minority Body: A Theory of Disability*. Oxford, UK: Oxford Univ. Press

Barsalou LW. 1999. Perceptual symbol systems. *Behav. Brain Sci.* 22(4):577–660

Bates E, Wulfeck B, MacWhinney B. 1991. Cross-linguistic research in aphasia: an overview. *Brain Lang.* 41(2):123–48

Bavelier D, Neville HJ. 2002. Cross-modal plasticity: where and how? *Nat. Rev. Neurosci.* 3(6):443–52

Bedny M. 2017. Evidence from blindness for a cognitively pluripotent cortex. *Trends Cogn. Sci.* 21(9):637–48

Bedny M, Caramazza A, Pascual-Leone A, Saxe R. 2012. Typical neural representations of action verbs develop without vision. *Cereb. Cortex* 22(2):286–93

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. *Curr. Biol.* 20(21):1900–6

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* 189:105–15

Bedny M, Pascual-Leone A, Dodell-Feder D, Fedorenko E, Saxe R. 2011. Language processing in the occipital cortex of congenitally blind adults. *PNAS* 108(11):4429–34

Bedny M, Pascual-Leone A, Saxe RR. 2009. Growing up blind does not change the neural bases of Theory of Mind. *PNAS* 106(27):11312–17

Bellugi U, Poizner H, Klima ES. 1989. Language, modality and the brain. *Trends Neurosci.* 12(10):380–88

Benedict R. 1935. *Patterns of Culture*. London: Routledge

Bengtsson SL, Haynes J-D, Sakai K, Buckley MJ, Passingham RE. 2009. The representation of abstract task rules in the human prefrontal cortex. *Cereb. Cortex* 19(8):1929–36

Ben-Shachar M, Dougherty RF, Deutsch GK, Wandell BA. 2011. The development of cortical sensitivity to visual word forms. *J. Cogn. Neurosci.* 23(9):2387–99

Bigelow A. 1987. Early words of blind children. *J. Child Lang.* 14(1):47–56

Boas F. 1896. The limitations of the comparative method of anthropology. *Science* 4(103):901–8

Bongard S, Nieder A. 2010. Basic mathematical rules are encoded by primate prefrontal cortex neurons. *PNAS* 107(5):2277–82

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

Bouhali F, Thiebaut de Schotten M, Pinel P, Poupon C, Mangin J-F, et al. 2014. Anatomical connections of the visual word form area. *J. Neurosci.* 34(46):15402–14

Boyd R, Richerson PJ, Henrich J. 2011. The cultural niche: why social learning is essential for human adaptation. *PNAS* 108(Suppl. 2):10918–25

Brannon EM, Merritt DJ. 2011. Evolutionary foundations of the approximate number system. In *Space, Time and Number in the Brain*, ed. S Dehaena, EM Brannon, pp. 207–24. London: Academic

Bressler SL, Tang W, Sylvester CM, Shulman GL, Corbetta M. 2008. Top-down control of human visual cortex by frontal and parietal cortex in anticipatory visual spatial attention. *J. Neurosci.* 28(40):10056–61

Broca P. 1861. Remarques sur le siége de la faculté du langage articulé, suivis d'une observation d'aphémie (perte de la parole). *Bull. Soc. Anat.* 6:330–57

Brookshire G, Lu J, Nusbaum HC, Goldin-Meadow S, Casasanto D. 2017. Visual cortex entrains to sign language. *PNAS* 114(24):6352–57

Bullmore E, Sporns O. 2012. The economy of brain network organization. *Nat. Rev. Neurosci.* 13(5):336–49

Bunge SA, Kahn I, Wallis JD, Miller EK, Wagner AD. 2003. Neural circuits subserving the retrieval and maintenance of abstract rules. *J. Neurophysiol.* 90(5):3419–28

Burton H. 2003. Visual cortex activity in early and late blind people. *J. Neurosci.* 23(10):4005–11

Burton H, Diamond JB, McDermott KB. 2003. Dissociating cortical regions activated by semantic and phonological tasks: a fMRI study in blind and sighted people. *J. Neurophysiol.* 90(3):1965–82

Burton H, Snyder AZ, Raichle ME. 2014. Resting state functional connectivity in early blind humans. *Front. Syst. Neurosci.* 8:51

Campbell EE, Bergelson E. 2022. Making sense of sensory language: acquisition of sensory knowledge by individuals with congenital sensory impairments. *Neuropsychologia* 174:108320

Campbell EE, Casillas R, Bergelson E. 2024. The role of vision in the acquisition of words: vocabulary development in blind toddlers. *Dev. Sci.* 27(4):e13475

Campbell R, MacSweeney M, Waters D. 2007. Sign language and the brain: a review. *J. Deaf Stud. Deaf Educ.* 13(1):3–20

Cantlon JF, Brannon EM. 2007. Basic math in monkeys and college students. *PLOS Biol.* 5(12):e328

Cantlon JF, Brannon EM. 2010. Animal arithmetic. In *Encyclopedia of Animal Behavior*, ed. N Clayton, pp. 55–62. Oxford, UK: Elsevier

Cantlon JF, Brannon EM, Carter EJ, Pelphrey KA. 2006. Functional imaging of numerical processing in adults and 4-y-old children. *PLOS Biol.* 4(5):e125

Cantlon JF, Libertus ME, Pinel P, Dehaene S, Brannon EM, Pelphrey KA. 2009. The neural development of an abstract concept of number. *J. Cogn. Neurosci.* 21(11):2217–29

Carey S. 2009. *The Origin of Concepts*. Oxford, UK: Oxford Univ. Press

Carey S, Barner D. 2019. Ontogenetic origins of human integer representations. *Trends Cogn. Sci.* 23(10):823–35

Carrigan EM, Coppola M. 2017. Successful communication does not drive language development: evidence from adult homesign. *Cognition* 158:10–27

Cavdaroglu S, Katz C, Knops A. 2015. Dissociating estimation from comparison and response eliminates parietal involvement in sequential numerosity perception. *NeuroImage* 116:135–48

Cesana-Arlotti N, Kovács ÁM, Téglás E. 2020. Infants recruit logic to learn about the social world. *Nat. Commun.* 11(1):5999

Cesana-Arlotti N, Martín A, Téglás E, Vorobyova L, Cetnarski R, Bonatti LL. 2018. Precursors of logical reasoning in preverbal human infants. *Science* 359(6381):1263–66

Cetron JS, Connolly AC, Diamond SG, May VV, Haxby JV, Kraemer DJM. 2020. Using the force: STEM knowledge and experience construct shared neural representations of engineering concepts. *NPJ Sci. Learn.* 5(1):6

Chandrasekaran B, Krishnan A, Gandour JT. 2007. Mismatch negativity to pitch contours is influenced by language experience. *Brain Res.* 1128:148–56

Cheng Q, Roth A, Halgren E, Mayberry RI. 2019. Effects of early language deprivation on brain connectivity: language pathways in deaf native and late first-language learners of American Sign Language. *Front. Hum. Neurosci.* 13:320

Chomsky N. 1965. *Aspects of the Theory of Syntax*. Cambridge, MA: MIT Press

Clark CA, Pritchard VE, Woodward LJ. 2010. Preschool executive functioning abilities predict early mathematics achievement. *Dev. Psychol.* 46(5):1176–91

Clark EV, Casillas M. 2015. First language acquisition. In *The Routledge Handbook of Linguistics*, ed. K Allan, pp. 311–28. London: Routledge

Clark JL. 2014. *Where I Stand: On the Signing Community and My DeafBlind Experience*. Minneapolis, MN: Handtype Press

Coetzee J, Monti M. 2018. At the core of reasoning: dissociating deductive and non-deductive load. *Hum. Brain Mapp.* 39(4):1850–61

Cohen LG, Celnik P, Pascual-Leone A, Corwell B, Faiz L, et al. 1997. Functional relevance of cross-modal plasticity in blind humans. *Nature* 389(6647):180–83

Cohen LG, Weeks RA, Sadato N, Celnik P, Ishii K, Hallett M. 1999. Period of susceptibility for cross-modal plasticity in the blind. *Ann. Neurol.* 45(4):451–60

Collignon O, Voss P, Lassonde M, Lepore F. 2009. Cross-modal plasticity for the spatial processing of sounds in visually deprived subjects. *Exp. Brain Res.* 192:343–58

Collins CE, Airey DC, Young NA, Leitch DB, Kaas JH. 2010. Neuron densities vary across and within cortical areas in primates. *PNAS* 107(36):15927–32

Comrie B. 1999. Grammatical gender systems: a linguist's assessment. *J. Psycholinguist. Res.* 28:457–66

Corballis MC. 1999. The gestural origins of language: human language may have evolved from manual gestures, which survive today as a "behavioral fossil" coupled to speech. *Am. Sci.* 87(2):138–45

Cragg L, Gilmore C. 2014. Skills underlying mathematics: the role of executive function in the development of mathematics proficiency. *Trends Neurosci. Educ.* 3(2):63–68

Crair MC, Gillespie DC, Stryker MP. 1998. The role of visual experience in the development of columns in cat visual cortex. *Science* 279(5350):566–70

Crollen V, Lazzouni L, Rezk M, Bellemare A, Lepore F, et al. 2019. Recruitment of the occipital cortex by arithmetic processing follows computational bias in the congenitally blind. *NeuroImage* 186:549–56

Crone EA, Wendelken C, Van Leijenhorst L, Honomichl RD, Christoff K, Bunge SA. 2009. Neurocognitive development of relational reasoning. *Dev. Sci.* 12(1):55–66

Damarla SR, Just MA. 2013. Decoding the representation of numerical values from brain activation patterns. *Hum. Brain Mapp.* 34(10):2624–34

Danker JF, Anderson JR. 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):1365–77

De Voogt A. 2021. The evolution of writing systems: an introduction. In *Oxford Handbook of Human Symbolic Evolution*, ed. N Gontier, A Lock, C Sinha, pp. 893–914. Oxford, UK: Oxford Univ. Press

Deen B, Saxe R, Bedny M. 2015. Occipital cortex of blind individuals is functionally coupled with executive control areas of frontal cortex. *J. Cogn. Neurosci.* 27(8):1633–47

Dehaene S, Cohen L. 2007. Cultural recycling of cortical maps. *Neuron* 56(2):384–98

Dehaene S, Cohen L. 2011. The unique role of the visual word form area in reading. *Trends Cogn. Sci.* 15(6):254–62

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):321–25

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 Biol.* 16(3):e2004103

Dryer MS. 2007. Word order. In *Language Typology and Syntactic Description*, Vol. 1, *Clause Structure*, ed. T Shopen, pp. 61–131. Cambridge, UK: Cambridge Univ. Press

Duncan J. 2010. The multiple-demand (MD) system of the primate brain: mental programs for intelligent behaviour. *Trends Cogn. Sci.* 14(4):172–79

Dunlea A. 1989. *Vision and the Emergence of Meaning: Blind and Sighted Children's Early Language*. Cambridge, UK: Cambridge Univ. Press

Durkheim E. 1947. *The Division of Labor in Society*, transl. George Simpson. New York: Free Press

Eger E, Michel V, Thirion B, Amadon A, Dehaene S, Kleinschmidt A. 2009. Deciphering cortical number coding from human brain activity patterns. *Curr. Biol.* 19(19):1608–15

Eiselt A-K, Nieder A. 2013. Representation of abstract quantitative rules applied to spatial and numerical magnitudes in primate prefrontal cortex. *J. Neurosci.* 33(17):7526–34

Emmorey K. 2001. Space on hand: the exploitation of signing space to illustrate abstract thought. In *Spatial Schemas and Abstract Thought*, ed. M Gattis, pp. 147–74. Cambridge, MA: MIT Press

Emmorey K. 2021. New perspectives on the neurobiology of sign languages. *Front. Commun.* 6:748430

Emmorey K, Corina D. 1990. Lexical recognition in sign language: effects of phonetic structure and morphology. *Percept. Mot. Skills* 71(Suppl. 3):1227–52

Emmorey K, Mehta S, McCullough S, Grabowski TJ. 2016. The neural circuits recruited for the production of signs and fingerspelled words. *Brain Lang.* 160:30–41

Enard W, Przeworski M, Fisher SE, Lai CSL, Wiebe V, et al. 2002. Molecular evolution of *FOXP2*, a gene involved in speech and language. *Nature* 418(6900):869–72

Epstein RA, Parker WE, Feiler AM. 2007. Where am I now? Distinct roles for parahippocampal and retrosplenial cortices in place recognition. *J. Neurosci.* 27(23):6141–49

Espinosa JS, Stryker MP. 2012. Development and plasticity of the primary visual cortex. *Neuron* 75(2):230–49

Evans N, Levinson SC. 2009. The myth of language universals: language diversity and its importance for cognitive science. *Behav. Brain Sci.* 32(5):429–48

Farghaly AA, El-Kafrawy PM. 2021. Exploring the use of cognitive tests to predict programming performance: a systematic literature review. In *2021 31st International Conference on Computer Theory and Applications (ICCTA)*, pp. 40–48. Piscataway, NJ: IEEE. **https://doi.org/10.1109/ICCTA54562.2021.9916610**

Fedorenko E, Behr MK, Kanwisher N. 2011. Functional specificity for high-level linguistic processing in the human brain. *PNAS* 108(39):16428–33

Fedorenko E, Duncan J, Kanwisher N. 2013. Broad domain generality in focal regions of frontal and parietal cortex. *PNAS* 110(41):16616–21

Fedorenko E, Ivanova A, Dhamala R, Bers MU. 2019. The language of programming: a cognitive perspective. *Trends Cogn. Sci.* 23(7):525–28

Fedorenko E, Varley R. 2016. Language and thought are not the same thing: evidence from neuroimaging and neurological patients. *Ann. N. Y. Acad. Sci.* 1369(1):132–53

Feigenson L, Dehaene S, Spelke E. 2004. Core systems of number. *Trends Cogn. Sci.* 8(7):307–14

Feiman R, Mody S, Carey S. 2022. The development of reasoning by exclusion in infancy. *Cogn. Psychol.* 135:101473

Ferjan-Ramirez N, Leonard MK, Torres C, Hatrak M, Halgren E, Mayberry RI. 2014. Neural language processing in adolescent first-language learners. *Cereb. Cortex* 24(10):2772–83

Finney EM, Fine I, Dobkins KR. 2001. Visual stimuli activate auditory cortex in the deaf. *Nat. Neurosci.* 4(12):1171–73

Fischer J, Price T. 2017. Meaning, intention, and inference in primate vocal communication. *Neurosci. Biobehav. Rev.* 82:22–31

Fitch WT, Hauser MD, 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 39th International Conference on Software Engineering, Buenos Aires, Argent., May 20–28

Forkel SJ, de Schotten MT, Kawadler JM, 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

Frank MC, Everett DL, Fedorenko E, Gibson E. 2008. Number as a cognitive technology: evidence from Pirahã language and cognition. *Cognition* 108(3):819–24

Friederici AD. 2009. Pathways to language: fiber tracts in the human brain. *Trends Cogn. Sci.* 13(4):175–81

Friedrich RM, Friederici AD. 2009. Mathematical logic in the human brain: syntax. *PLOS ONE* 4(5):e5599

Friedrich RM, Friederici AD. 2013. Mathematical logic in the human brain: semantics. *PLOS ONE* 8(1):e53699

Gallese V, Lakoff G. 2005. The brain's concepts: the role of the sensory-motor system in conceptual knowledge. *Cogn. Neuropsychol.* 22(3–4):455–79

Gelman SA. 2009. Learning from others: children's construction of concepts. *Annu. Rev. Psychol.* 60:115–40

Gilbert CD, Li W. 2013. Top-down influences on visual processing. *Nat. Rev. Neurosci.* 14(5):350–63

Gleitman L, Newport E. 1995. The invention of language by children: environmental and biological influences on the acquisition of language. In *An Invitation to Cognitive Science*, Vol. 1: *Language*, ed. L Gleitman, M Liberman, pp. 1–24. Cambridge, MA: MIT Press. 2nd ed.

Goel V. 2007. Anatomy of deductive reasoning. *Trends Cogn. Sci.* 11(10):435–41

Gogtay N, Giedd JN, Lusk L, Hayashi KM, Greenstein D, et al. 2004. Dynamic mapping of human cortical development during childhood through early adulthood. *PNAS* 101(21):8174–79

Goldin-Meadow S. 2005. *The Resilience of Language: What Gesture Creation in Deaf Children Can Tell Us About How All Children Learn Language*. New York: Psychology Press

Gopnik A, Wellman HM. 1992. Why the child's theory of mind really is a theory. *Mind Lang*. 7(1–2):145–71

Gordon P. 2004. Numerical cognition without words: evidence from Amazonia. *Science* 306(5695):496–99

Granda A, Nuccio J. 2018. *Protactile Principles*. Monmouth, OR: Tactile Commun.

Greenough WT, Black JE, Wallace CS. 1987. Experience and brain development. *Child Dev*. 58(3):539–59

Grill-Spector K, Malach R. 2004. The human visual cortex. *Annu. Rev. Neurosci.* 27:649–77

Gurnee W, Tegmark M. 2024. Language models represent space and time. arXiv:2310.02207 [cs.LG]

Gweon H. 2021. Inferential social learning: cognitive foundations of human social learning and teaching. *Trends Cogn. Sci.* 25(10):896–910

Hall WC. 2017. What you don't know can hurt you: the risk of language deprivation by impairing sign language development in deaf children. *Matern. Child Health J.* 21(5):961–65

Harris PL, Koenig MA. 2006. Trust in testimony: how children learn about science and religion. *Child Dev*. 77(3):505–24

Hartley CA. 2022. How do natural environments shape adaptive cognition across the lifespan? *Trends Cogn. Sci.* 26(12):1029–30

Hartley CA, Nussenbaum K, Cohen AO. 2021. Interactive development of adaptive learning and memory. *Annu. Rev. Dev. Psychol.* 3:59–85

Hartshorne JK, Tenenbaum JB, Pinker S. 2018. A critical period for second language acquisition: evidence from 2/3 million English speakers. *Cognition* 177:263–77

Hauptman M, Elli G, Pant R, Bedny M. 2023. Neural specialization for 'visual' concepts emerges in the absence of vision. bioRxiv 2023.08.23.552701. **https://doi.org/10.1101/2023.08.23.552701**

Henrich J, McElreath R. 2003. The evolution of cultural evolution. *Evol. Anthropol.* 12(3):123–35

Hensch TK. 2004. Critical period regulation. *Annu. Rev. Neurosci.* 27:549–79

Hensch TK. 2005. Critical period plasticity in local cortical circuits. *Nat. Rev. Neurosci.* 6(11):877–88

Hensch TK. 2018. Critical periods in cortical development. In *The Neurobiology of Brain and Behavioral Development*, ed. R Gibb, B Kolb, pp. 133–51. London: Academic

Heyes C. 2018. *Cognitive Gadgets: The Cultural Evolution of Thinking*. Cambridge, MA: Harvard Univ. Press

Hickok G, Bellugi U, Klima ES. 1996. The neurobiology of sign language and its implications for the neural basis of language. *Nature* 381(6584):699–702

Hickok G, Poeppel D, Clark K, Buxton RB, Rowley HA, Roberts TPL. 1997. Sensory mapping in a congenitally deaf subject: MEG and fRMI studies of cross-modal non-plasticity. *Hum. Brain Mapp.* 5(6):437–44

Hirshorn EA, Li Y, Ward MJ, Richardson RM, Fiez JA, Ghuman AS. 2016. Decoding and disrupting left midfusiform gyrus activity during word reading. *PNAS* 113(29):8162–67

Holloway ID, Battista C, Vogel SE, Ansari D. 2013. Semantic and perceptual processing of number symbols: evidence from a cross-linguistic fMRI adaptation study. *J. Cogn. Neurosci.* 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. *J. Neurophysiol.* 83(4):2355–73

Hubel DH, Wiesel TN. 1970. The period of susceptibility to the physiological effects of unilateral eye closure in kittens. *J. Physiol.* 206(2):419–36

Hume D. 1740. *An Abstract of a Treatise of Human Nature*. Hamden, CT: Archon Books

Huttenlocher PR. 2009. *Neural Plasticity: The Effects of Environment on the Development of the Cerebral Cortex*. Cambridge, MA: Harvard Univ. Press

Huttenlocher PR, Dabholkar AS. 1997. Regional differences in synaptogenesis in human cerebral cortex. *J. Comp. Neurol.* 387(2):167–78

Ikutani Y, Kubo T, Nishida S, Hata H, Matsumoto K, et al. 2021. Expert programmers have fine-tuned cortical representations of source code. *eNeuro* 8(1):ENEURO.0405-20.2020

Isik L, Koldewyn K, Beeler D, Kanwisher N. 2017. Perceiving social interactions in the posterior superior temporal sulcus. *PNAS* 114(43):E9145–52

Ivanova AA, Srikant S, Sueoka Y, Kean HH, Dhamala R, et al. 2020. Comprehension of computer code relies primarily on domain-general executive brain regions. *eLife* 9:e58906

Johnson JS, Newport EL. 1989. Critical period effects in second language learning: the influence of maturational state on the acquisition of English as a second language. *Cogn. Psychol.* 21(1):60–99

Jorstad NL, Close J, Johansen N, Yanny AM, Barkan ER, et al. 2023. Transcriptomic cytoarchitecture reveals principles of human neocortex organization. *Science* 382(6667):eadf6812

Kadosh RC, Kadosh KC, Kaas A, Henik A, Goebel R. 2007. Notation-dependent and-independent representations of numbers in the parietal lobes. *Neuron* 53(2):307–14

Kahn DM, Krubitzer L. 2002. Massive cross-modal cortical plasticity and the emergence of a new cortical area in developmentally blind mammals. *PNAS* 99(17):11429–34

Kanjlia S, Feigenson L, Bedny M. 2021. Neural basis of approximate number in congenital blindness. *Cortex* 142:342–56

Kanjlia S, Lane C, Feigenson L, Bedny M. 2016. Absence of visual experience modifies the neural basis of numerical thinking. *PNAS* 113(40):11172–77

Kanwisher N, McDermott J, Chun MM. 1997. The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J. Neurosci.* 17:4302–11

Kanwisher N, Yovel G. 2006. The fusiform face area: a cortical region specialized for the perception of faces. *Philos. Trans. R. Soc. B* 361(1476):2109–28

Kim JS, Aheimer B, Montané Manrara V, Bedny M. 2021. Shared understanding of color among sighted and blind adults. *PNAS* 118(33):e2020192118

Kim JS, Elli GV, Bedny M. 2019. Knowledge of animal appearance among sighted and blind adults. *PNAS* 116(23):11213–22

Kitayama S, Park J. 2010. Cultural neuroscience of the self: understanding the social grounding of the brain. *Soc. Cogn. Affect. Neurosci.* 5(2–3):111–29

Klima ES, Bellugi U. 1979. *The Signs of Language*. Cambridge, MA: Harvard Univ. Press

Kocab A, Senghas A, Snedeker J. 2016. The emergence of temporal language in Nicaraguan Sign Language. *Cognition* 156:147–63

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

Krubitzer L. 1995. The organization of neocortex in mammals: Are species differences really so different? *Trends Neurosci*. 18(9):408–17

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), Seoul, Korea, June 27–July 19

Kupers R, Pappens M, de Noordhout AM, Schoenen J, Ptito M, Fumal A. 2007. rTMS of the occipital cortex abolishes Braille reading and repetition priming in blind subjects. *Neurology* 68(9):691–93

Kyttälä M, Lehto JE. 2008. Some factors underlying mathematical performance: the role of visuospatial working memory and non-verbal intelligence. *Eur. J. Psychol. Educ.* 23:77–94

Lai CSL, Fisher SE, Hurst JA, Vargha-Khadem F, Monaco AP. 2001. A forkhead-domain gene is mutated in a severe speech and language disorder. *Nature* 413(6855):519–23

Landau B, Gleitman LR. 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. *J. Neurosci.* 35(37):12859–68

Larsen B, Luna B. 2018. Adolescence as a neurobiological critical period for the development of higher-order cognition. *Neurosci. Biobehav. Rev.* 94:179–95

Legare CH. 2017. Cumulative cultural learning: development and diversity. *PNAS* 114(30):7877–83

Legare CH, Gelman SA. 2008. Bewitchment, biology, or both: the co-existence of natural and supernatural explanatory frameworks across development. *Cogn. Sci.* 32(4):607–42

Lenneberg EH. 1967. The biological foundations of language. *Hosp. Pract.* 2(12):59–67

Leslie AM, Gelman R, Gallistel CR. 2008. The generative basis of natural number concepts. *Trends Cogn. Sci.* 12(6):213–18

Lewis LB, Saenz M, Fine I. 2010. Mechanisms of cross-modal plasticity in early-blind subjects. *J. Neurophysiol.* 104(6):2995–3008

Lewis TL, Maurer D. 2005. Multiple sensitive periods in human visual development: evidence from visually deprived children. *Dev. Psychobiol.* 46(3):163–83

Libertus ME, Feigenson L, Halberda J. 2011. Preschool acuity of the approximate number system correlates with school math ability. *Dev. Sci.* 14(6):1292–300

Lillo-Martin D, Henner J. 2021. Acquisition of sign languages. *Annu. Rev. Linguist.* 7:395–419

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 Lang*. 251:105392

Locke J. 1690. *An Essay Concerning Human Understanding*. London: Ward, Lock & Co. New ed.

Lupyan G, Rakison DH, McClelland JL. 2007. Language is not just for talking: Redundant labels facilitate learning of novel categories. *Psychol. Sci.* 18(12):1077–83

Lutz DJ, Keil FC. 2002. Early understanding of the division of cognitive labor. *Child Dev*. 73(4):1073–84

Mackey A, Miller Singley A, Bunge S. 2013. Intensive reasoning training alters patterns of brain connectivity at rest. *J. Neurosci.* 33(11):4796–803

MacSweeney M, Capek CM, Campbell R, Woll B. 2008a. The signing brain: the neurobiology of sign language. *Trends Cogn. Sci.* 12(11):432–40

MacSweeney M, Waters D, Brammer MJ, Woll B, Goswami U. 2008b. Phonological processing in deaf signers and the impact of age of first language acquisition. *NeuroImage* 40(3):1369–79

Majid A, Roberts SG, Cilissen L, Emmorey K, Nicodemus B, et al. 2018. Differential coding of perception in the world’s languages. *PNAS* 115(45):11369–76

Makin TR, Krakauer JW. 2023. Against cortical reorganisation. *eLife* 12:e84716

Malik-Moraleda S, Ayyash D, Gallée J, Affourtit J, Hoffmann M, et al. 2022. An investigation across 45 languages and 12 language families reveals a universal language network. *Nat. Neurosci.* 25(8):1014–19

Marjieh R, Sucholutsky I, van Rijn P, Jacoby N, Griffiths T. 2023. What language reveals about perception: distilling psychophysical knowledge from large language models. *Proc. Annu. Meet. Cogn. Sci. Society* 45. **https://escholarship.org/uc/item/6dk5q565**

Marmor GS. 1978. Age at onset of blindness and the development of the semantics of color names. *J. Exp. Child Psychol.* 25(2):267–78

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):1444–60

Maurer D, Werker JF. 2014. Perceptual narrowing during infancy: a comparison of language and faces. *Dev. Psychobiol.* 56(2):154–78

Mayberry RI, Kluender R. 2018. Rethinking the critical period for language: new insights into an old question from American Sign Language. *Biling. Lang. Cogn.* 21(5):886–905

McNeill D. 2012. *How Language Began: Gesture and Speech in Human Evolution*. Cambridge, UK: Cambridge Univ. Press

Mead M. 1928. The role of the individual in Samoan culture. *J. R. Anthropol. Inst. G. B. Ireland* 58:481–95

Mellor CM. 2006. *Louis Braille: A Touch of Genius*. Boston, MA: Natl. Braille Press

Millar S. 1984. Is there a "best hand" for Braille? *Cortex* 20(1):75–87

Millar S. 2003. *Reading by Touch*. London: 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 Res.* 1714:133–46

Monti M, Parsons L, Osherson D. 2009. The boundaries of language and thought in deductive inference. *PNAS* 106(30):12554–59

Morishita H, Hensch TK. 2008. Critical period revisited: impact on vision. *Curr. Opin. Neurobiol.* 18(1):101–7

Musz E, Loiotile R, Chen J, Bedny M. 2023. Naturalistic audio-movies reveal common spatial organization across "visual" cortices of different blind individuals. *Cereb. 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

Nakai T, Sakai KL. 2014. Neural mechanisms underlying the computation of hierarchical tree structures in mathematics. *PLOS ONE* 9(11):e111439

Neville HJ, Coffey SA, Lawson DS, Fischer A, Emmorey K, Bellugi U. 1997. Neural systems mediating American Sign Language: effects of sensory experience and age of acquisition. *Brain Lang.* 57(3):285–308

Newport EL. 1990. Maturational constraints on language learning. *Cogn. Sci.* 14(1):11–28

Nieder A. 2021a. Neuroethology of number sense across the animal kingdom. *J. Exp. Biol.* 224(6):jeb218289

Nieder A. 2021b. The evolutionary history of brains for numbers. *Trends Cogn. Sci.* 25(7):608–21

Nieder A, Dehaene S. 2009. Representation of number in the brain. *Annu. Rev. Neurosci.* 32:185–208

Noppeney U, Friston KJ, Price CJ. 2003. Effects of visual deprivation on the organization of the semantic system. *Brain* 126(7):1620–27

Obretenova S, Halko MA, Plow EB, Pascual-Leone A, Merabet LB. 2010. Neuroplasticity associated with tactile language communication in a deaf-blind subject. *Front. Hum. Neurosci.* 3:953

Oomen M, Kimmelman V. 2019. Body-anchored verbs and argument omission in two sign languages. *Glossa* 4(1):42

Padden CA, Humphries TL. 2006. *Inside Deaf Culture*. Cambridge, MA: Harvard Univ. Press

Park H-J, Friston K. 2013. Structural and functional brain networks: from connections to cognition. *Science* 342(6158):1238411

Pascual-Leone A, Amedi A, Fregni F, Merabet LB. 2005. The plastic human brain cortex. *Annu. Rev. Neurosci.* 28:377–401

Passingham RE, Stephan KE, Kötter R. 2002. The anatomical basis of functional localization in the cortex. *Nat. Rev. Neurosci.* 3(8):606–16

Perniss P, Pfau R, Steinbach M. 2007. Can't you see the difference? Sources of variation in sign language structure. *Trends Linguist. Stud. Monogr.* 188:1–34

Petersen SE, Sporns O. 2015. Brain networks and cognitive architectures. *Neuron* 88(1):207–19

Petroni F, Rocktäschel T, Lewis P, Bakhtin A, Wu Y, et al. 2019. Language models as knowledge bases? arXiv:1909.01066 [cs.CL]

Piazza M, Eger E. 2016. Neural foundations and functional specificity of number representations. *Neuropsychologia* 83:257–73

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

Pinker S. 2010. The cognitive niche: coevolution of intelligence, sociality, and language. *PNAS* 107:8993–99

Pizzorusso T, Medini P, Berardi N, Chierzi S, Fawcett JW, Maffei L. 2002. Reactivation of ocular dominance plasticity in the adult visual cortex. *Science* 298(5596):1248–51

Poirier C, Collignon O, Scheiber C, Renier L, Vanlierde A, et al. 2006. Auditory motion perception activates visual motion areas in early blind subjects. *NeuroImage* 31(1):279–85

Pollick AS, de Waal FBM. 2007. Ape gestures and language evolution. *PNAS* 104(19):8184–89

Potts R. 1998. Variability selection in hominid evolution. *Evol. Anthropol.* 7(3):81–96

Prabhakaran V, Smith JA, Desmond JE, Glover GH, Gabrieli JD. 1997. Neural substrates of fluid reasoning: an fMRI study of neocortical activation during performance of the Raven's Progressive Matrices Test. *Cogn. Psychol.* 33(1):43–63

Prat CS, Madhyastha TM, Mottarella MJ, Kuo C-H. 2020. Relating natural language aptitude to individual differences in learning programming languages. *Sci. Rep.* 10(1):3817

Price C, Wise R, Frackowiak R. 1996. Demonstrating the implicit processing of visually presented words and pseudowords. *Cereb. Cortex* 6(1):62–70

Purcell JJ, Napoliello EM, Eden GF. 2011. A combined fMRI study of typed spelling and reading. *NeuroImage* 55(2):750–62

Qin W, Yu C. 2013. Neural pathways conveying novisual information to the visual cortex. *Neural Plast*. 2013:864920

Quartz SR, Sejnowski TJ. 1997. The neural basis of cognitive development: a constructivist manifesto. *Behav. Brain Sci.* 20(4):537–56

Raven J. 1965. *Advanced Progressive Matrices. Sets I and II*. London: HK Lewis

Raz G, Saxe R. 2020. Learning in infancy is active, endogenously motivated, and depends on the prefrontal cortices. *Annu. Rev. Dev. Psychol.* 2:247–68

Reich L, Szwed M, Cohen L, Amedi A. 2011. A ventral visual stream reading center independent of visual experience. *Curr. Biol.* 21(5):363–68

Reilly J. 2006. How faces come to serve grammar: the development of nonmanual morphology in American Sign Language. In *Advances in the Sign Language Development of Deaf Children*, ed. B Schick, M Marschark, PE Spencer, pp. 262–90. Oxford, UK: Oxford Univ. Press

Richardson H, Koster-Hale J, Caselli N, Magid R, Benedict R, et al. 2020. Reduced neural selectivity for mental states in deaf children with delayed exposure to sign language. *Nat. Commun.* 11(1):3246

Roberts P, Stewart BA. 2018. Defining the 'generalist specialist' niche for Pleistocene *Homo sapiens*. *Nat. Hum. Behav.* 2(8):542–50

Röder B, Rösler F, Hennighausen E, Näcker F. 1996. Event-related potentials during auditory and somatosensory discrimination in sighted and blind human subjects. *Cogn. Brain Res.* 4(2):77–93

Röder B, Stock O, Bien S, Neville H, Rösler F. 2002. Speech processing activates visual cortex in congenitally blind humans. *Eur. J. Neurosci.* 16(5):930–36

Saccone EJ, Tian M, Bedny M. 2024. Developing cortex is functionally pluripotent: evidence from blindness. *Dev. Cogn. Neurosci.* 66:101360

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 MP, Ibañez V, Hallett M. 1998. Neural networks for Braille reading by the blind. *Brain* 121(7):1213–29

Sadato N, Pascual-Leone A, Grafman J, Ibañez V, Deiber M-P, et al. 1996. Activation of the primary visual cortex by Braille reading in blind subjects. *Nature* 380(6574):526–28

Saxe R. 2006. Uniquely human social cognition. *Curr. Opin. Neurobiol.* 16(2):235–39

Saxe R, Kanwisher N. 2003. People thinking about thinking people: the role of the temporo-parietal junction in "theory of mind." *NeuroImage* 19(4):1835–42

Saygin ZM, Osher DE, Norton ES, Youssoufian DA, Beach SD, et al. 2016. Connectivity precedes function in the development of the visual word form area. *Nat. Neurosci.* 19(9):1250–55

Saysani A, Corballis MC, Corballis PM. 2018. Colour envisioned: concepts of colour in the blind and sighted. *Vis. Cogn.* 26(5):382–92

Schaefer A, Kong R, Gordon EM, Laumann TO, Zuo XN, et al. 2018. Local-global parcellation of the human cerebral cortex from intrinsic functional connectivity MRI. *Cereb. Cortex* 28(9):3095–114

Schmandt-Besserat D, Erard M. 2008. Origins and forms of writing. In *Handbook of Research on Writing*, ed. C Bazerman, pp. 7–26. New York: Routledge

Senju A, Csibra G. 2008. Gaze following in human infants depends on communicative signals. *Curr. Biol.* 18(9):668–71

Shepard RN, Cooper LA. 1992. Representation of colors in the blind, color-blind, and normally sighted. *Psychol. Sci.* 3(2):97–104

Sherwood CC, Gómez-Robles A. 2017. Brain plasticity and human evolution. *Annu. Rev. Anthropol.* 46:399–419

Shum J, Fanda L, Dugan P, Doyle WK, Devinsky O, Flinker A. 2020. Neural correlates of sign language production revealed by electrocorticography. *Neurology* 95(21):e2880–89

Shuman M, Kanwisher N. 2004. Numerical magnitude in the human parietal lobe: tests of representational generality and domain specificity. *Neuron* 44(3):557–69

Siegmund J, Kästner C, Apel S, Parnin C, Bethmann A, et al. 2014. *Understanding understanding source code with functional magnetic resonance imaging*. Paper presented at the 36th International Conference on Software Engineering, Hyderabad, India, May 31–June 7

Spaepen E, Coppola M, Spelke ES, Carey SE, Goldin-Meadow S. 2011. Number without a language model. *PNAS* 108(8):3163–68

Spelke ES. 2017. Core knowledge, language, and number. *Lang. Learn. Dev.* 13(2):147–70

Spelke ES. 2022. *What Babies Know: Core Knowledge and Composition*, Vol. 1. New York: Oxford Univ. Press

Sporns O. 2022. The complex brain: connectivity, dynamics, information. *Trends Cogn. Sci.* 26(12):1066–67

Srikant S, Lipkin B, Ivanova AA, Fedorenko E, O'Reilly U-M. 2022. *Convergent representations of computer programs in human and artificial neural networks*. Paper presented at the 36th Annual Conference on Neural Information Processing Systems, New Orleans, LA, Nov 28–Dec 9

Striem-Amit E, Ovadia-Caro S, Caramazza A, Margulies DS, Villringer A, Amedi A. 2015. Functional connectivity of visual cortex in the blind follows retinotopic organization principles. *Brain* 138(6):1679–95

Striem-Amit E, Wang X, Bi Y, Caramazza A. 2018. Neural representation of visual concepts in people born blind. *Nat. Commun.* 9(1):5250

Szwed M, Dehaene S, Kleinschmidt A, Eger E, Valabrègue R, et al. 2011. Specialization for written words over objects in the visual cortex. *NeuroImage* 56(1):330–44

Tennie C, Call J, Tomasello M. 2009. Ratcheting up the ratchet: on the evolution of cumulative culture. *Philos. Trans. R. Soc. B* 364(1528):2405–15

Terrace HS, Petitto LA, Sanders RJ, Bever TG. 1979. Can an ape create a sentence? *Science* 206(4421):891–902

Thompson-Schill SL, D'Esposito M, Aguirre GK, Farah MJ. 1997. Role of left inferior prefrontal cortex in retrieval of semantic knowledge: a reevaluation. *PNAS* 94(26):14792–97

Thompson-Schill SL, Ramscar M, Chrysikou EG. 2009. Cognition without control: when a little frontal lobe goes a long way. *Curr. Dir. Psychol. Sci.* 18(5):259–63

Tian M, Saccone EJ, Kim JS, Kanjlia S, Bedny M. 2023. Sensory modality and spoken language shape reading network in blind readers of Braille. *Cereb. Cortex* 33(6):2426–40

Tian M, Xiao X, Hu H, Cusack R, Bedny M. 2024. Visual experience shapes functional connectivity between occipital and non-visual networks. *eLife* 13:RP93067. Preprint. **https://doi.org/10.7554/eLife.93067.1**

Tomasello M. 1999. The human adaptation for culture. *Annu. Rev. Anthropol.* 28:509–29

Tomasello M. 2010. *Origins of Human Communication*. Cambridge, MA: MIT Press

Tooby J, Cosmides L. 1992. The psychological foundations of culture. In *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*, ed. JH Barkow, L Cosmides, J Trooby, pp. 19–136. New York: Oxford Univ. Press

Tooby J, DeVore I. 1987. The reconstruction of hominid behavioral evolution through strategic modeling. In *The Evolution of Human Behavior: Primate Models*, ed. WG Kinzey, pp. 183–237. 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. *J. Neurophysiol.* 101(6):2984–94

Van Den Heuvel MP, Sporns O. 2011. Rich-club organization of the human connectome. *J. Neurosci.* 31(44):15775–86

Vendrell P, Junqué C, Pujol J, Jurado MA, Molet J, Grafman J. 1995. The role of prefrontal regions in the Stroop task. *Neuropsychologia* 33(3):341–52

Vinckier F, Dehaene S, Jobert A, Dubus JP, 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):143–56

Von Melchner L, Pallas SL, Sur M. 2000. Visual behaviour mediated by retinal projections directed to the auditory pathway. *Nature* 404(6780):871–76

Wallis JD, Anderson KC, Miller EK. 2001. Single neurons in prefrontal cortex encode abstract rules. *Nature* 411(6840):953–56

Wanet-Defalque M-C, Veraart C, De Volder A, Metz R, Michel C, et al. 1988. High metabolic activity in the visual cortex of early blind human subjects. *Brain Res.* 446(2):369–73

Wang J, Halberda J, Feigenson L. 2017. Approximate number sense correlates with math performance in gifted adolescents. *Acta Psychol.* 176:78–84

Wang X, Men W, Gao J, Caramazza A, Bi Y. 2020. Two forms of knowledge representations in the human brain. *Neuron* 107(2):383–93.e5

Weiner KS, Barnett MA, Lorenz S, Caspers J, Stigliani A, et al. 2017. The cytoarchitecture of domain-specific regions in human high-level visual cortex. *Cereb. Cortex* 27(1):146–61

Wellman HM, Carey S, Gleitman L, Newport EL, Spelke ES. 1990. *The Child's Theory of Mind*. Cambridge, MA: MIT Press

Werchan DM, Collins AG, Frank MJ, Amso D. 2016. Role of prefrontal cortex in learning and generalizing hierarchical rules in 8-month-old infants. *J. Neurosci.* 36(40):10314–22

Werker JF, Hensch TK. 2015. Critical periods in speech perception: new directions. *Annu. Rev. Psychol.* 66:173–96

Wolbers T, Zahorik P, Giudice NA. 2011. Decoding the direction of auditory motion in blind humans. *NeuroImage* 56(2):681–87

Woll B. 2018. The consequences of very late exposure to BSL as an L1. *Biling. Lang. Cogn.* 21(5):936–37

Woll B, Sutton-Spence R, Elton F. 2001. Multilingualism: the global approach to sign languages. In *The Sociolinguistics of Sign Language*, ed. C Lucas, pp. 8–32. Cambridge, UK: Cambridge Univ. Press

Woodward AL. 1998. Infants selectively encode the goal object of an actor's reach. *Cognition* 69(1):1–34

Woodward JC. 1972. Implications for sociolinguistic research among the deaf. *Sign Lang. Stud.* 1:1–7

Woolgar A, Jackson J, Duncan J. 2016. Coding of visual, auditory, rule, and response information in the brain: 10 years of multivoxel pattern analysis. *J. Cogn. Neurosci.* 28(10):1433–54

Wright S, Matlen B, Baym C, Ferrer E, Bunge S. 2008. Neural correlates of fluid reasoning in children and adults. *Front. Hum. Neurosci.* 1:8

Xu F, Spelke ES, Goddard S. 2005. Number sense in human infants. *Dev. Sci.* 8(1):88–101

Xu M, Baldauf D, Chang CQ, Desimone R, Tan LH. 2017. Distinct distributed patterns of neural activity are associated with two languages in the bilingual brain. *Sci. Adv.* 3(7):e1603309

Xu S, Li Y, Liu J. 2021. The neural correlates of computational thinking: collaboration of distinct cognitive components revealed by fMRI. *Cereb. Cortex* 31(12):5579–97

Yang C. 2013. Ontogeny and phylogeny of language. *PNAS* 110(16):6324–27

Yaple ZA, Stevens WD, 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 MSY, Zdunek S, Bergmann O, Bernard S, Salehpour M, et al. 2014. Dynamics of oligodendrocyte generation and myelination in the human brain. *Cell* 159(4):766–74

Zeller E, Timmermann A, Yun KS, Raia P, Stein K, Ruan J. 2023. Human adaptation to diverse biomes over the past 3 million years. *Science* 380(6645):604–8

Zimmermann M, Cusack R, Bedny M, Szwed M. 2024. Auditory areas are recruited for naturalistic visual meaning in early deaf people. *Nat. Commun.* 15:8035