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MIND, BRAIN, AND EDUCATION

The Virtuous Cycle between Education and Neuroscience

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ABSTRACT— Educational neuroscience was born out of the promise that brain imaging would generate discoveries that change how we educate our children. Many neuroscientists and educators alike feel that this promise has not been fulfilled and have begun to question the utility of this nascent field that is arising at the intersection of two well-established disciplines. We argue that discoveries in educational neuroscience should be considered from a holistic perspective, and we should not only ask "how can neuroscience contribute to education practice?," but also "how can the study of education inform our understanding of the human brain?" Rather than expecting a one-way street from the lab to the classroom, we should strive for a virtuous cycle between education and neuroscience, and embrace interdisciplinary discoveries that would not be possible within the traditional confines of either discipline. The combination of education interventions with neuroscience methodologies is redefining our understanding of plasticity in the human brain and has already elucidated mechanisms by which a child's environment sculpts brain circuits to achieve incredible new capacities like literacy.

A fundamental question in neuroscience is how experience shapes the structure and function of the brain. This question can be addressed by education interventions, which offer a unique opportunity to test how experimental manipulations of the environment impact brain development, thus answering basic scientific questions about experience-dependent plasticity in the human brain (Economou et al., 2022, 2023; Huber, Donnelly, Rokem, & Yeatman, 2018; Huber, Mezer, & Yeatman, 2021; Keller & Just, 2009; Meisler, Gabrieli, & Christodoulou, 2024; Yeatman et al., 2024). A fundamental question in education is why academic outcomes vary so dramatically among children given the same educational environment (curriculum, teacher, etc.). Brain imaging measures offer a unique opportunity to understand the mechanisms underlying individual differences in learning trajectories and guide progress toward personalized education. Here, we present the case that embracing a virtuous cycle between education and neuroscience can generate discoveries that would not be possible within the confines of either discipline.

Critics of the emerging field of educational neuroscience have questioned whether neuroscience has made any meaningful contributions to education (Bowers, 2016; Bruer, 1997, 2016; Howard-Jones, 2014; Howard-Jones et al., 2016). For example, Bowers asserts that "changes in brain states are irrelevant to evaluating the efficacy of instruction. What matters is not whether the brain changes, but whether the child learns as expressed in behavior" (Bowers, 2016). While, on the one hand, we agree with this point—the goal of education is to teach students skills regardless of the brain mechanism that supports learning—we also think that this is an overly narrow perspective to take on interdisciplinary research. When considering the promises and pitfalls of interdisciplinary research, rather than asking what one field can contribute to the other, we should be asking how the two disciplines can be integrated to bolster new discoveries. Thus, rather than expecting educational neuroscience to offer an immediate solution to challenges in the classroom, we should appreciate the potential for synergy between education and neuroscience (Fischer et al., 2010; Thomas, Ansari, & Knowland, 2019). Combining cognitive neuroscience methods with education interventions has already generated fundamental discoveries about the human brain that would not otherwise have been possible. In the coming years, these data can be leveraged to explore the promises and pitfalls of "Precision Education."

Whether or not neuroscience informs specific classroom practices, the scientific discoveries that emerge from this research will carry value for educators and scientists

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alike. For example, knowing that a learning challenge (e.g., dyslexia) is grounded in neurobiological differences makes us understand the student's challenge in a deeper way. Data demonstrating that differences in specific brain structures as early as infancy predict some, but not all, variance in learning outcomes provides a nuanced perspective on the interaction between child-specific factors and the learning environment. Further, knowing whether the neurobiology is or is not malleable (i.e., plastic) will affect our approach to supporting these children.

The following sections make the case that education offers a unique opportunity to study causality in human neuroscience. We then highlight discoveries from one of the most extensively studied aspects of education, reading, and dyslexia, that have broad importance for the field of neuroscience. Currently, the fundamental discoveries in educational neuroscience outpace their readiness for applied or translational science, let alone direct classroom application. As the field matures, applied science should increasingly leverage these basic scientific findings to create a beneficial feedback loop and inspire a virtuous cycle between education and neuroscience.

UNDERSTANDING THE CAUSAL LINK BETWEEN NEURAL RESPONSES AND BEHAVIOR

The ultimate test of any model describing the relationship between neural computations and behavior is to experimentally manipulate either neural activity or behavior and measure how changing one affects the other. Optogenetics and other invasive techniques afford researchers working in animal models experimental control over neural activity, making it possible to test whether changes in neural activity cause changes in behavior (Boyden, Zhang, Bamberg, Nagel, & Deisseroth, 2005; Deisseroth, 2011). The power of these techniques for testing causal models has ushered in a paradigm shift in our understanding of neural circuits and behavior in mice. In animal research, it is similarly possible to fully control the environment and examine how different experiences induce long-lasting changes in the brain. Consider, for example, foundational studies where animals were deprived of a specific type of input (e.g., suturing an eye shut or depriving them of seeing any face), which resulted in fundamental reorganization of the visual system (Arcaro, Schade, Vincent, Ponce, & Livingstone, 2017; Hubel & Wiesel, 1963; Rauschecker & Korte, 1993). However, even though rodents and nonhuman primates can serve as a model of basic mechanisms of plasticity, they cannot elucidate the neural underpinnings of the myriad of important, uniquely human behaviors like reading, language, mathematics, complex social interactions, and emotion regulation, to name a few (Silverman et al., 2022). These invasive methods of perturbing either the brain or the environment are generally not ethical or feasible in humans. How then can we make inferences about causality in humans?

CAUSALITY IN HUMAN NEUROSCIENCE

The very first discoveries regarding the neurobiology of language were observations made by neurologists studying patients recovering from stroke (Broca, 1861; Wernicke, 1874). These case studies provided important insights into the location of brain regions supporting language. For example, in the 1860s and 1870s, we learned that language is left-hemisphere dominant and that different aspects of language are compartmentalized in the frontal and temporal lobes (Broca, 1861; Geschwind, 1970; Wernicke, 1874). This is an example of a natural experiment where the brain suffers an injury, and the researcher examines the effect of the injury on language and cognitive function. However, a natural experiment affords far less control than a true experiment.

More recently, the development of noninvasive imaging methods has allowed researchers to examine brain function in populations that suffer from congenital conditions affecting sensory experience, like the congenitally blind, deaf, and people born without one of their hands. This line of research has led to new understandings of the striking degree of functional reorganization of the sensory and motor cortices (Bedny, Pascual-Leone, Dodell-Feder, Fedorenko, & Saxe, 2011; Finney, Fine, & Dobkins, 2001; Hahamy et al., 2017; Zimmermann, Cusack, Bedny, & Szwed, 2024). These, too, are examples of natural experiments where either the brain or the environment is dramatically altered, allowing researchers to make hypotheses about causality. While they provide important insights, they are limited in several critical aspects: they are uncontrolled, there is immense variation in the location, severity, and extent of the affected regions, they are (fortunately) rare, and they only allow the study of scenarios of deprivation. In other words, natural experiments open a window into loss of function rather than gain of function (learning).

These limitations are addressed by training studies that aim to examine learning-induced brain plasticity (both in terms of structural and functional changes) in a controlled way. Whereas learning is measured based on changes in behavior, plasticity refers to experience-dependent changes in brain structure and/or function and can be measured based on MRI, MEG, or EEG data collection immediately before and after a training paradigm. Using diffusion MRI, these types of studies have shown promising effects, relating rapid changes in brain structure to controlled experiences (Hofstetter, Friedmann, & Assaf, 2017; Keller & Just, 2016; Sagi et al., 2012; Stee et al., 2023; Tavor, Botvinik-Nezer, Bernstein-Eliav, Tsarfaty, & Assaf, 2020). However, it remains unclear whether there are long-term effects of

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this type of short-term training, both in terms of behavioral gains and neurobiological changes. Further, these studies are typically characterized by small sample sizes, as it is difficult to recruit volunteer participants for the substantial time commitment required by multiple training and scanning sessions. Educational interventions address these challenges and provide an unparalleled opportunity to examine learning-induced plasticity in humans, with large effect sizes, and in terms of uniquely human behaviors. Combining neuroscientific measurements with intervention designs leverages a natural setting where participants master a new skill, often over timescales ranging from weeks to months to years. We argue that harnessing education programs, and targeted interventions in particular, has implications for neuroscience research that goes beyond the field of education per se. Rather, they can serve as a unique lens into causal mechanisms of plasticity and learning in humans.

For example, Meshulam and colleagues collected fMRI data in college students in a computer programming class while they were watching recorded lectures several times during the semester (Meshulam et al., 2021). They found that the degree of alignment in the neural activation patterns between each student and the average group pattern was associated with subsequently better learning outcomes. Another recent study leveraged an elective high school course to examine whether intensive learning of spatial cognition skills transferred to other, untrained, skills, like verbal reasoning (Cortes et al., 2022). They found that not only did neural change predict learning transfer it did so better than any combination of behavioral assessments. In both these examples, the overarching research questions did not necessarily concern the specific content of instruction but rather capitalized on the educational settings to address general questions about mechanisms of learning. In the next sections, we highlight how reading intervention studies have contributed to the broad understanding of learning-induced plasticity. We focus on reading instruction as a special case of education interventions, as it is a skill that has become necessary for daily life, is critical for academic success, and typically requires years of formal schooling to master. We begin with evidence regarding white matter plasticity—changes in the physical structure of the brain's axonal connections—as children master reading skills.

EDUCATION SCULPTS WHITE MATTER DEVELOPMENT

Twenty years ago, many cognitive neuroscientists would ascribe to the belief that white matter and other non-neuronal tissue, such as glial cells are the static infrastructure of the brain, mature early in life, and are largely unrelated to cognition and learning. However, two sets of fundamental observations about the white matter have spurred a sea change in cognitive neuroscience: (1) In humans, diffusion-weighted magnetic resonance imaging (dMRI) revealed that white matter tissue properties are linked to individual differences in many aspects of cognitive function and academic performance (Saygin et al., 2013; Travis, Leitner, Feldman, & Ben-Shachar, 2015; Tsang, Dougherty, Deutsch, Wandell, & Ben-Shachar, 2009; Vandermosten et al., 2012; Vanderauwera, Vandermosten, Dell'Acqua, Wouters, & Ghesquière, 2015; Wandell & Yeatman, 2013; Yablonski, Rastle, Taylor, & Ben-Shachar, 2019; Yeatman et al., 2011; Yeatman, Dougherty, Ben-Shachar, & Wandell, 2012). (2) In animal models, molecular and cellular measures revealed that oligodendrocytes, the glial cells that are responsible for myelination in the white matter, actively monitor neural activity through signaling mechanisms that sense nerve discharges, allowing them to adjust axon properties in response to neural activity (Bacmeister et al., 2022; Barres & Raff, 1993; Gibson et al., 2014; McKenzie et al., 2014). In other words, there is an active cellular feedback loop for white matter architecture to be sculpted by experience (Barres, 2008; Fields, 2005; Pease-Raissi & Chan, 2021). Indeed, it is now largely appreciated that the white matter not only plays an essential role in behavior, but also that plasticity in the white matter is a critical component of the learning process (Fields, 2015).

Despite the emerging consensus on the critical role of white matter plasticity in learning, there remains a disconnect between the animal literature, which has used elegant experiments to detail the cell types that actively change with experience, and the human literature, which is primarily dominated by correlational studies. Correlational studies, unfortunately, cannot shed light on the dynamic interplay between white matter plasticity and human learning (Roy et al., 2024). One of the reasons for this gap is the inherent difficulty of conducting causal manipulations in humans, as described in the previous section. Thus, while the animal literature paints a picture of white matter as a dynamic system that rapidly responds and changes as a function of environmental factors (Almeida & Lyons, 2017), far less is known about the time course and mechanisms of human white matter plasticity. Educational interventions (either through changes implemented in the classroom or researcher-designed interventions conducted outside a formal education setting) can fill this void by providing a paradigm in which researchers can implement dramatic changes to the environment, with tight experimental control over variables that are deemed important for learning, and with opportunities for large-dosage interventions that are carried out over protracted periods of time. These types of studies can provide an unparalleled window into the time course of neural changes and how these changes are expressed in uniquely human behaviors. The training intensity that is possible in an educational intervention is also

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unmatched by other experimental paradigms that are appropriate for humans (e.g., perceptual learning (Li, 2016; Sasaki, Nanez, & Watanabe, 2010)), allowing educational neuroscience researchers much larger effects to work with. Thus, educational neuroscience can open a unique window into the mechanisms of human brain plasticity.

For example, Huber and colleagues enrolled children with dyslexia in an intensive reading intervention program that involved a high dosage (4 h a day), delivered at regular time intervals (5 days a week), over an extended period of time (8 weeks), and made regular measurements of the white matter with diffusion MRI (Huber et al., 2018). This intensive training paradigm revealed that white matter plasticity occurs much more rapidly, over a larger spatial scale, and with a larger effect size than previously believed (Figure 1).

The behavioral data revealed a linear dose–response function with reading skills improving incrementally with each hour of intervention (Donnelly et al., 2019). The brain imaging data revealed changes in the structure of major white matter connections that could be detected within the first 2 weeks of intervention. Moreover, an individual's time course of white matter plasticity tracked their time course of learning, meaning that variability in children's response to intervention is linked to mechanisms of plasticity (though the direction of causality is, of course, unknown). The relationship between intensive reading intervention and white matter plasticity has now seen replication across independent labs (Meisler et al., 2024).

Two surprising findings emerged from these studies that have important implications for both neuroscientists and

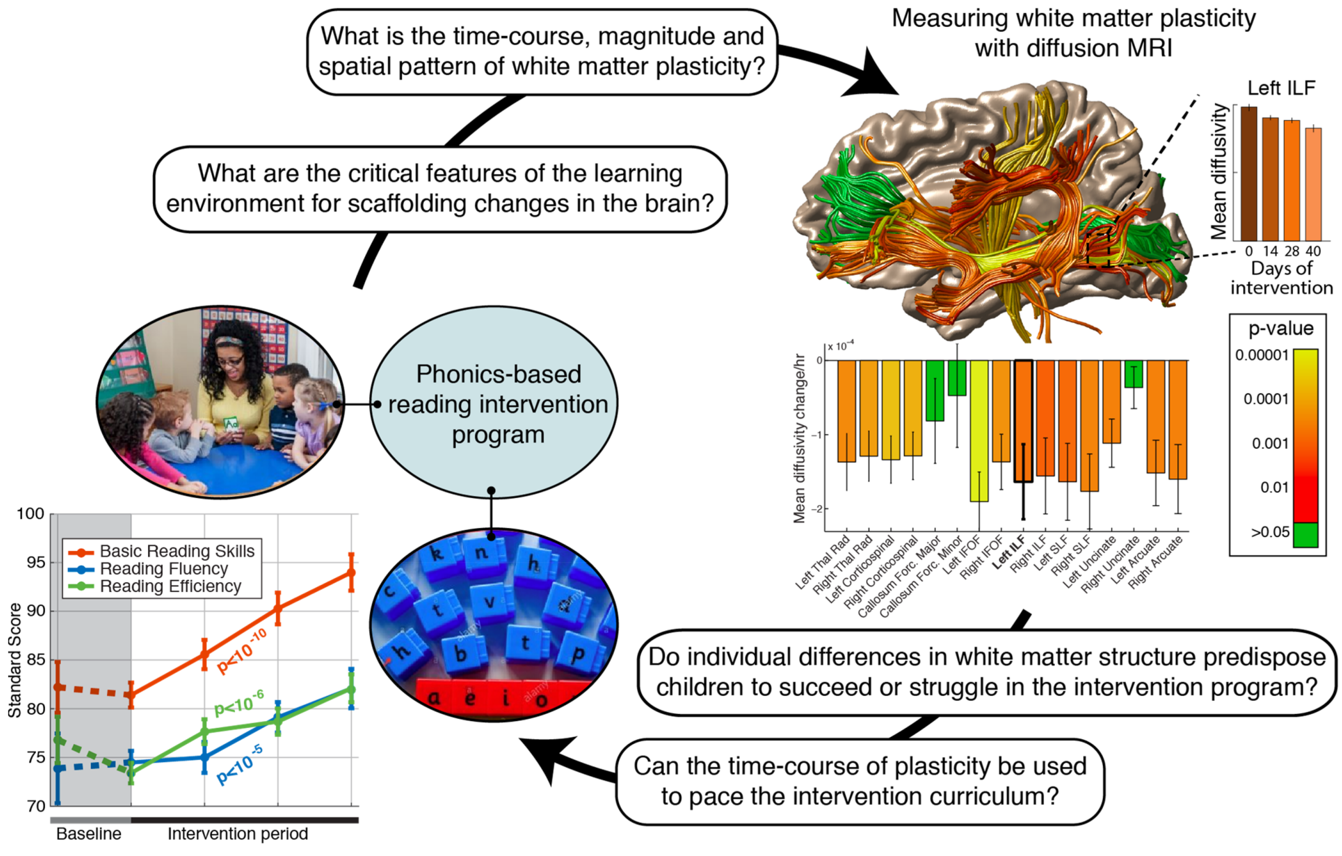

Fig. 1. The virtuous cycle between education and neuroscience. Interdisciplinary research catalyzes discoveries that are not possible within the traditional confines of a discipline. For example, combining a highly effective, intensive dyslexia intervention with longitudinal quantitative MRI measures of white matter tissue properties opens a window into the mechanisms of plasticity in the human brain. Data from Donnelly, Huber, and Yeatman (2019)) (lower left) show how an intensive summer intervention program can drive large (effect sizes ranging from 0.8 to 1.2), roughly linear growth in reading skills. By combining this type of education intervention with dMRI and other quantitative MRI measurements (Huber et al., 2018, 2021; Mezer et al., 2013), we can ask basic scientific questions about the principles of brain plasticity. Data from Huber et al. (2018; upper right) show the time course of changes in white matter structure and how plasticity was distributed across an extensive network of white matter tracts. Over the coming years and decades, these types of neurobiological measures can be used to inform our understanding of learning differences. Along the way to closing this virtuous cycle, we can expect many influential discoveries.

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educators. First was the observation that changes occurred across a distributed network of white matter connections and were not localized to a single, specific white matter tract. As the intervention targeted reading skills, we might have expected changes to be isolated to the core connections of the brain's reading circuitry. However, for children with dyslexia, successful interventions involve more than just training on reading skills. For many children with dyslexia, school is a daily struggle. Reading is a source of anxiety, and as children progress through the grades, reading becomes ubiquitous. For example, even math transitions to word problems. Many children with dyslexia develop a negative self-concept, struggle to find a sense of belonging in school, and have significantly higher rates of clinically diagnosed anxiety and depression (Georgiou, Parrila, & McArthur, 2024; Nelson & Gregg, 2012; Novita, 2016; Sanfilippo et al., 2020; Zuppardo, Serrano, Pirrone, & Rodriguez-Fuentes, 2023). A successful intervention program must overcome these challenges and prove to the child that they can be successful in the area that is the largest challenge in their life. Thus, beyond training on reading specifically, successful interventions involve many aspects of social–emotional learning, changes in mindset, and more broadly, a dramatic change to the day-to-day negative experiences in school. What we do not know is the extent to which rapid and extensive white matter plasticity reflects the learning of reading skills specifically, versus the multitude of new experiences that are encapsulated in the intervention.

The second surprising observation was the effect size: over 8 weeks of intensive intervention, both reading skills and white matter diffusion properties changed by roughly 1 standard deviation. As a point of reference, the typical group comparison of dyslexic versus typical readers reports group differences of roughly 0.2 standard deviations on most brain metrics (though more recent studies suggest that group differences might reflect sampling biases (Roy et al., 2024)). This means that group differences on most brain metrics are smaller than the brain's capacity for experience-driven change, an observation that overturns the long-held belief by many scientists and educators that dyslexia reflects a "defect" in the brain that cannot be changed. Rather, high-quality intervention programs can inspire large-scale changes in brain structure that occur over a rapid timescale and in synchrony with growth in reading skills. Which systems are plastic and malleable to intervention, and which are stable, remains an open question that has far-reaching implications for Neuroscience (Wandell & Smirnakis, 2009), as well as for education. Future research harnessing carefully designed interventions may shed light on the extent, time course, and constraints on plasticity, and whether there are specific conditions for plasticity to occur.

Future advances in quantitative MRI can bridge the gap between the mechanistic, cellular-level measures that are possible in animal research and the resolution available in human neuroimaging. For example, Huber et al. (2021) found that rapid intervention-driven changes in white matter likely reflect proliferation of glial cells, rather than myelination per se. In another literacy intervention study, Economou et al. (2022, 2023) found intervention-driven changes in white matter using an index of myelin that were not observed using traditional diffusion metrics. These examples demonstrate how emerging quantitative MRI methods can generate testable hypotheses regarding the cellular mechanisms of plasticity and learning in humans (Bridge & Clare, 2006; Mezer et al., 2013; Stikov et al., 2015; Weiskopf, Edwards, Helms, Mohammadi, & Kirilina, 2021; Yeatman, Wandell, & Mezer, 2014). Recent efforts to shorten scan duration will allow more longitudinal studies in children to incorporate these quantitative measures (Cao, Liao, Iyer, Wang, & Zhou, 2022; Yablonski et al., 2024).

NEUROSCIENCE SHEDS LIGHT ON MULTIPLE PATHWAYS TO LEARNING

A long-standing debate in education centers around the question of "normalization" versus "compensation": do struggling readers improve their reading by strengthening the impaired skills, or do they recruit alternative pathways that differ from the general population to bypass their deficits? The neuroscience of education interventions can shed light on this question by projecting these competing hypotheses onto well-documented brain circuits and examining where intervention-driven changes occur. In the context of reading, years of neuroscience research have described a well-characterized circuit (Pugh et al., 1996; Yeatman & White, 2021), and a specific component of this circuit, the visual word form area (VWFA), is considered the hallmark of literacy (Dehaene et al., 2011; Dehaene, Cohen, Morais, & Kolinsky, 2015). The VWFA is located in the left hemisphere ventral occipitotemporal cortex (VOTC) and selectively responds to written words in literate adults. This word-selective response is absent in illiterate adults (Dehaene et al., 2011) and prereading children (Dehaene-Lambertz, Monzalvo, & Dehaene, 2018; Feng, Monzalvo, Dehaene, & Dehaene-Lambertz, 2022). The response properties of the VWFA correlate with reading skills (Ben-Shachar, Dougherty, Deutsch, & Wandell, 2011; Brem et al., 2020; Centanni et al., 2018; Kubota, Joo, Huber, & Yeatman, 2019), and in people with dyslexia, the VWFA is the most common location of differences in neural responses (Richlan, 2020; Richlan, Kronbichler, & Wimmer, 2011). Moreover, lesions to the left VOTC because of stroke (Philipose et al., 2007; Turkeltaub et al., 2014) or surgical resection (Gaillard et al., 2006) cause profound

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reading impairments in adults. By all counts, the VWFA is intricately tied to skilled reading; thus, incrementally improving reading skills through a targeted training program should lead to a predictable change in the neural response of this region.

However, now that there have been more than 20 studies that have measured fMRI responses over the course of interventions in children and adults with dyslexia (Barquero, Davis, & Cutting, 2014; Perdue et al., 2022), it is clear that the story is more nuanced than we would have predicted. While some intervention studies report increases in the VWFA response (Brem et al., 2010; Eden et al., 2004; Heim, Pape-Neumann, van Ermingen-Marbach, Brinkhaus, & Grande, 2015; Shaywitz et al., 2004; Yeatman et al., 2024), others do not (Meyler, Keller, Cherkassky, Gabrieli, & Just, 2008; Odegard, Ring, Smith, Biggan, & Black, 2008; Partanen, Siegel, & Giaschi, 2019). Moreover, some studies report changes in right hemisphere regions that are not typically associated with reading (Nugiel et al., 2019; Partanen et al., 2019). These right hemisphere activations have been termed "compensatory mechanisms" because they appear to develop in some people with dyslexia who overcome their reading challenges. However, as many aspects of spoken language are lateralized to the left hemisphere, there are reasons to believe that right hemisphere compensatory mechanisms might not be as efficient as the typical, left-lateralized reading circuitry. Similarly, when considering the role of white matter, one might expect that effective reading intervention would lead to white matter tracts becoming more similar to those of typical readers. However, Huber et al. (2018) found the opposite: successful reading intervention drove white matter properties further away from those of typical readers, thereby increasing group differences rather than reducing them. Thus, this collection of education interventions has demonstrated that proficient reading can be achieved through multiple neural pathways, even though there is a well-defined canonical reading circuit. This is a case where the synergy between neuroscience and education has led to insights that could not be uncovered based on measuring behavioral improvement alone. Even though the basic science is not mature enough for direct application to classroom practices, it provides a foundation to begin building and testing new hypotheses that could, eventually, be translated to applications.

PREDICTION: HOW NEURAL MEASURES CAN PROVIDE UNIQUE INSIGHTS INTO LEARNING DIFFERENCES

The notion that mastering a complicated behavior like reading can be achieved via multiple pathways is also supported by longitudinal studies that investigated individual differences in prereading children who later become struggling readers. Several studies that followed children at risk of dyslexia have identified brain differences prior to school entry between children at risk who later develop typical reading skills and those at risk who continue to struggle (Van der Auwera, Wouters, Van der Mosten, & Ghesquière, 2017; Wang et al., 2017; Zuk et al., 2021). For example, Zuk et al. (2021) found that children deemed at risk for dyslexia in kindergarten who continued to struggle with reading into second grade showed similar white matter profiles to typical readers. In contrast, children at risk who subsequently developed typical reading skills showed markedly different white matter properties in the right hemisphere as early as kindergarten (Zuk et al., 2021). This counterintuitive finding suggests a biological marker for resilience or for developing alternative pathways to skilled reading. The presence of these differences before learning to read suggests that they are not the result of impoverished reading experience or of the struggles associated with having dyslexia (though they could reflect infant and preschool experience). Importantly, longitudinal studies also find that neural measures predict learning outcomes above and beyond behavioral measures (Bach, Richardson, Brandeis, Martin, & Brem, 2013; Borchers et al., 2019; Hoeft et al., 2011; Kraft et al., 2016; Myers et al., 2014; Raschle, Zuk, & Gaab, 2012; Wang et al., 2017; Zuk et al., 2021). The same has been reported in educational intervention studies: individual differences in response to intervention are sometimes better predicted by baseline brain measures than by behavioral measures (Cortes et al., 2022; Karipidis et al., 2018; Rezaie et al., 2011; Supekar et al., 2013). Together, these findings suggest that brain measurements offer insights into individual differences in learning trajectories and might explain variability in response to intervention (Gabrieli, Ghosh, & Whitfield-Gabrieli, 2015). Brain measurements are able to capture variance in learning outcomes that are not yet captured by well-established, traditional screening measures. The variability revealed by these studies highlights the importance of characterizing the subtle differences in reading behavior that might manifest among individuals who have developed different neural circuits to support skilled reading. Insights from brain imaging may inform the development of more sensitive behavioral measures and direct the spotlight of research and instruction to areas that require additional support. For example, McNorgan, Alvarez, Bhullar, Gayda, and Booth (2011) found that reading outcomes were predicted by activation in different brain regions in younger and older children, which may suggest that interventions should target different sub-skills of reading at different ages. Thus, even though brain imaging metrics are not an outcome measure that a school or parent should routinely use to make educational decisions, they can (1) shed light on mechanisms of learning that might not be obvious from behavioral measures alone

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and (2) highlight the relationship between learning and other systems (e.g., memory, attention) or environmental factors and give rise to new hypotheses and approaches to intervention. As the basic science matures, critical opportunities for impactful applied science will emerge, inspiring new approaches to intervention that can be tested in an applied context.

CONCLUSIONS

In sum, educational interventions can be a powerful tool to investigate the interplay between brain plasticity and cognition in humans. We argue that harnessing educational settings—and particularly interventions—can lead to insights with broad implications for our understanding of the human brain. Interventions bridge the gap between manipulations possible in animal research and the constraints of human cognitive neuroscience, thus allowing researchers to make inferences about causality. Moreover, neuroscience can advance our understanding of individual differences in learning, response to intervention, and remediation of learning challenges (Gabrieli, 2016; Park & Mackey, 2022). We propose to view this virtuous cycle as a reciprocal relationship that bridges the gap between the two disciplines.

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CONFLICT OF INTEREST

The authors have no conflict of interest to report.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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