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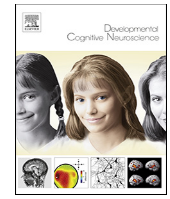

The role of the visual association cortex in scaffolding prefrontal cortex development: A novel mechanism linking socioeconomic status and executive function

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ABSTRACT

Socioeconomic status (SES) is associated with executive function (EF) and prefrontal cortex (PFC) development. However, understanding of the specific aspects of SES that influence development of EF and the PFC remains limited. We briefly review existing literature on proposed mechanisms linking SES with EF. Then, we present a novel conceptual model arguing that early cognitive stimulation shapes EF and PFC development. We propose that cognitive stimulation drives lower-level sensory and perceptual processes that may impact EF and PFC development through reciprocal connections between the ventral visual stream and PFC. We argue that caregivers guide attention and associative learning, which provides children the opportunity to regulate attention and gain semantic knowledge. This experience in turn allows for opportunities to train the PFC to resolve conflict between stimuli with overlapping features and engage in increasingly complex computations as visual processing systems develop; this may lay the groundwork for development of EF. We review existing evidence for this model and end by highlighting how this conceptual model could launch future research questions.

The prefrontal cortex (PFC) is involved in multiple forms of higher-order cognition, including working memory, conflict monitoring, inhibitory control, and shifting between rule sets (Botvinick et al., 2004; Miyake and Friedman, 2012; Miyake et al., 2001). These cognitive processes are collectively referred to as executive functions (EF). Together these skills allow the formation and execution of future-oriented plans and the inhibition of behaviors that do not serve these plans, providing the foundation for healthy decision-making and self-regulation.

EF in early childhood is associated with school readiness (Blair, 2002), academic success (Blair and Razza, 2007), risky behaviors in adolescence and adulthood (Crews and Boettiger, 2009; Patrick et al., 2008), the likelihood of becoming incarcerated (Yechiam et al., 2008), and a wide range of outcomes in adulthood in the domains of health, socioeconomic status (SES), and criminal behavior, over and above the effects of IQ (Moffitt et al., 2011). Determining how early environmental experiences shape EF development is critical to identifying educational, community, and family-based strategies to nurture and support the development of these skills and promote healthy outcomes across the life span. We argue that accelerated progress in this effort can be made only when intervention development is informed by a principled and biologically plausible understanding of the developmental mechanisms by which environmental experience shapes the development of the PFC and associated EF. In this piece, we review the existing literature on how early environmental experiences shape EF outcomes, and then offer a novel perspective on how these experiences may be shaping the PFC and EF beginning in infancy.

1. Environmental influences on EF and PFC development

Environmental experience shapes developmental processes through experience-expectant and experience-dependent processes (Greenough et al., 1987). Experience-expectant learning is best illustrated in relation to sensory system development. The neural circuits that process sensory information are sculpted by specific environmental inputs during sensitive periods early in development. For example, populations of neurons in visual cortex are well-matched to properties of patterned light input from the environment (Hubel and Wiesel, 1968,1974,2012). In typical development, sound and light information is similarly available to all animals, driving very similar and species-

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typical patterns of cortical development in sensory networks—or experience-expectant processes. Experience-dependent plasticity, in contrast, reflects emergent connections between neuronal populations in a way that reflects each person's unique environmental experiences. Long-term memory is a classic example of experience-dependent plasticity, where the process of long-term memory formation is shared across individuals but specific memories differ across individuals based on experience. Similarly, infants may experience more or fewer objects of various colors in the home and this variability may impact color processing and object perception development (Werchan et al., 2019). Our focus here is on experience-dependent learning and the impact that this variability of experiences has on PFC and EF development.

Considerable evidence suggests that environmental experience plays a meaningful role in the development of PFC and EF, although the specific experience-dependent processes involved remain largely unknown. Evidence for the importance of early environmental experience in shaping PFC and EF development comes from the well-documented reductions in EF ability among children who have experienced an absence of stable and responsive caregiving, such as institutional rearing and neglect (Bos, 2009; McLaughlin et al., 2017; Pollak et al., 2010; Tibu et al., 2016). Childhood SES—including parental education and income—is also associated with individual differences in EF, such that higher SES is associated with better EF performance; critically, this association is observable across the entire SES distribution and is not present only in children living in poverty (Amso and Lynn, 2017; Hackman et al., 2015; Lengua et al., 2014; Rosen et al., 2018; Sarsour et al., 2012). SES is also associated with structure and function of the PFC (Finn et al., 2016; Hair et al., 2015; Noble et al., 2007; Rosen et al., 2018; Sheridan et al., 2012) and this association exists across the entire SES distribution (e.g.,Noble et al., 2015; Amso and Lynn, 2017; Rosen et al., 2018; Lawson et al., 2013). Differences in structure and function of the PFC are also observed in extreme circumstances of caregiver deprivation as in neglect and institutional rearing, (e.g., Mueller et al., 2010; Hodel et al., 2015).

Given the established link between variability in PFC-dependent EF development with caregiving and childhood SES, identifying specific types of experiences that are required for adaptive EF and PFC development is a goal of many research studies (Hackman et al., 2015; Kolb et al., 2012). However, unlike experience-expectant inputs that are critical in sensory development, there is unlikely to be a singular set of specific environmental experiences that is required optimal PFC development. Indeed, a recent model of PFC argues that PFC development reflects *adaptation* to the child's changing environment (Werchan and Amso, 2017), an experience-dependent rather than experience-expectant process. Below, we articulate a novel conceptual account of how specific early environmental experiences that are associated with childhood SES could impact experience-dependent learning and in turn produce lasting differences in EF and PFC development.

2. Existing models of environmental experience and EF development

The link between SES and EF is almost certainly multifactorial, involving a variety of mechanisms operating at multiple levels of influence. Here we review some mechanistic explanations that have been previously proposed. For instance, it has been proposed that children reared in poverty lack rules, routines, and structure, and that the environments of children from low-SES families are more "chaotic," disorganized, and unstable (Evans & Wachs, 2009). In turn, this lack of structure, consistency, and routines is thought to produce poor EF (Evans et al., 2005; Hart et al., 2007; Hughes & Ensor, 2009; Vernon-Feagans et al., 2016). Additionally, it has often been suggested that exposure to high levels of stress has a deleterious effect on PFC function (Hackman & Farah, 2009; Hanson et al., 2010; Lupien et al., 2009) in ways that ultimately constrain EF (Blair et al., 2011).

Although each of these models has some empirical support, they are limited in their ability to explain the types of environmental experiences that are required to develop adaptive EF and support PFC development. For example, although exposure to stress may impair PFC function, a stress account provides insufficient explanation for the types of experiences that are required for the PFC to develop the capacity for EF (i.e., an absence of stress does not sufficiently describe the types of experiences that scaffold EF development). The strongest support for these proposed mechanisms comes from studies of children living in poverty (Blair et al., 2011). However, as SES increases, features of the environment that tend to co-occur with poverty—including stress and chaos—are generally mitigated. In other words, differences in EF among children from economically stable middle-class families as compared to wealthy families is unlikely to be explained by greater levels of stress or chaos in the children from middle-class families (Hart et al., 2007; Turner and Avison, 2003; Turner and Lloyd, 1995; Hatch and Dohrenwend, 2007); yet, SES-related differences in EF and PFC are well-documented even at the upper end of the SES distribution (Amso et al., 2018; Noble et al., 2005; Noble et al., 2007; Sarsour et al., 2012; Rosen et al., 2018). As such, explanations focused on stress and chaos cannot account fully for why EF and PFC structure and function vary along the entire SES gradient. Rather, they are explanations as to why we might expect to see disparities among youths raised in poverty or in more extreme adverse environments compared to children raised in more advantaged circumstances.

We focus on the role of cognitive stimulation as a mechanism linking SES and EF, building on other recent conceptual models (Hackman et al., 2010; Sheridan and McLaughlin, 2014). Cognitive stimulation is characterized by access to a complex environment with developmentally appropriate learning materials, a rich variety of experiences, a complex linguistic environment, and the presence of a caregiver who interacts with the child consistently and uses strategies that promote learning (e.g. scaffolding). Access to complex sensory, linguistic, motoric, and social experiences that occur in the context of caregiver interactions have been argued to shape the early forms of learning that scaffold the development of more complex forms of cognition, including EF (McLaughlin et al., 2017). We argue that cognitive stimulation supports development of the feed-forward and feedback loops between sensory processing regions and the PFC, which lays the groundwork for the complex computations necessary for EF (Werchan and Amso, 2017).

In contrast to other proposed mechanistic explanations, cognitive stimulation accounts for the association between SES and EF across the entire SES distribution and highlights specific types of experiences that are likely to scaffold development of the PFC. Cognitive stimulation and the complexity of early linguistic experience have been associated with the development of EF and PFC structure and function in multiple studies (Hackman et al., 2010; Rosen et al., 2018; Sarsour et al., 2012; Sheridan et al., 2012; Rosen et al., In Press), and mediate the association of SES with EF and PFC structure, even after adjustment for exposure to stress or violence (Hackman et al., 2015; Rosen et al., 2018; Rosen et al., In Press). Differences in cognitive stimulation may contribute to EF disparities among children exposed to adversity, given the well-established reductions in cognitive stimulation observed among children exposed to caregiver deprivation and from low-SES households (Bradley and Corwyn, 2002; Bradley et al., 2001; Hart and Risley, 1995; Kantor et al., 2004; Smyke et al., 2007). Critically, however, cognitive stimulation varies across the entire SES distribution—with children from higher-SES households experiencing more cognitive stimulation even at the highest end of the SES distribution—and is associated with individual differences in EF (Bradley et al., 2001; Hackman et al., 2015; Rosen et al., 2018; Rosen et al., In Press; Amso et al., 2019), making this a plausible environmental mechanism explaining variation in EF and PFC function.

Other aspects of early experience encompassed in our definition of cognitive stimulation also vary across the SES distribution and predict EF, including language exposure and parent scaffolding of child

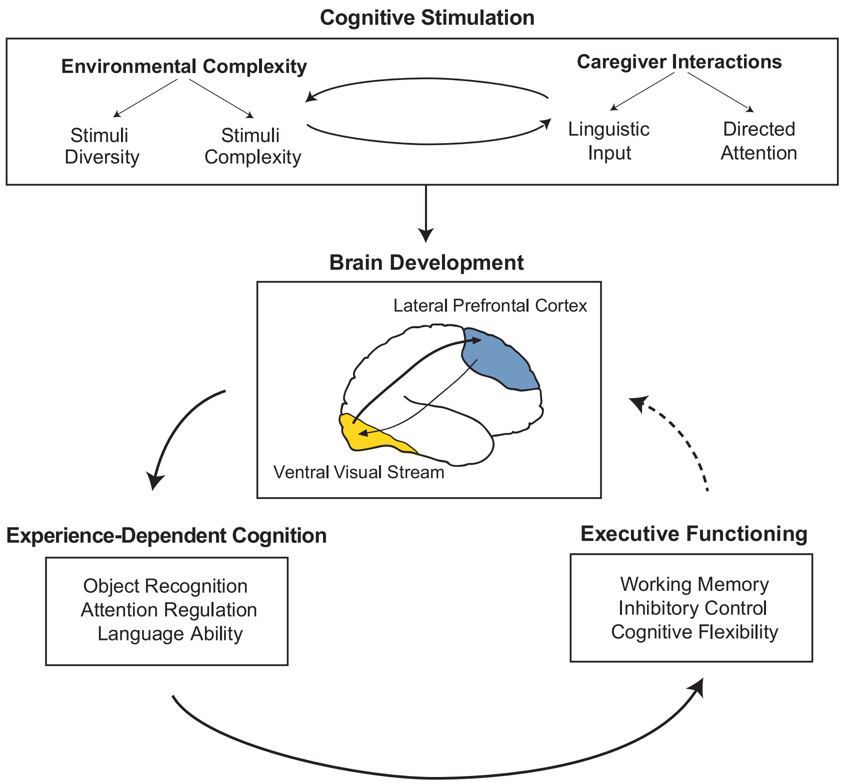

Fig. 1. Conceptual model. Illustration of how cognitive stimulation, including access to a complex environment with developmentally appropriate learning materials and a variety of experiences, a complex linguistic environment, and a caregiver who engages in behavior to promote learning, may explain differences in prefrontal cortex (PFC) and executive function by driving reciprocal interactions between the ventral visual stream and the PFC.

learning. Caregiver language quality and quantity increase across the entire SES distribution (Gilkerson et al., 2017; Hart and Risley, 1995; Romeo et al., 2018; Rowe, 2012) and contribute to SES-related differences in neurocognitive development, including EF (Ursache and Noble, 2016). Parental scaffolding provides a structure and framework in which children have the tools to learn while letting the child explore and work toward independence (Vygotsky, 1978; Wood et al., 1976) and is a specific dimension of parenting thought to be important in the development of EF (Lengua et al., 2007, 2014). Parental scaffolding varies as a function of SES, such that higher SES parents tend to provide more scaffolding than their lower SES counterparts (Blair and Raver, 2012; Lengua et al., 2014). Scaffolding is seen as an external guide for children to direct and switch attention (Bibok et al., 2009). Maternal verbal scaffolding predicts better verbal abilities in children, which in turn affords children greater facility with language in guiding their own behavior (Landry et al., 2002). Some suggest that scaffolding coupled with secure attachment where children can feel comfortable exploring and trying new solutions explains variation in children's EF (Carlson, 2009). Individual differences in scaffolding strongly predict EF ability and this holds true over and above the effect of SES (Blair et al., 2014; Fay-Stammbach et al., 2014; Lengua et al., 2007; Sosic-Vasic et al., 2017; Hammond et al., 2012).

Importantly, parenting is a complex construct including many elements across emotional, cognitive, and social domains (Collins et al., 2000; Maccoby and Martin, 1983; Mermelshtine, 2017). Here, we focus specifically on the degree to which parents interact with their children in ways that support child learning. This includes both the quantity of interaction as well as the quality of that interaction (e.g., linguistic complexity, and use of specific strategies that promote learning, like scaffolding). Many other aspects of parenting do not, in our view, reflect cognitive stimulation – such as warmth, responsiveness, predictability, discipline strategies, and many others.

Together, this body of literature suggests that variation in multiple components of cognitive stimulation including environmental complexity, variety of experiences, linguistic exposure, and parental involvement in child learning are plausible mechanisms explaining SES-related disparities in EF.

3. A novel account: scaffolded perceptual experience drives EF and PFC development

Here we integrate and expand on these existing mechanistic models in a novel conceptual model with testable hypotheses. Specifically, we advance a model that posits a central role of interaction with caregivers early in development in shaping EF and PFC development. In this section, we dissect how high level cognitive stimulation may drive lower-level sensory and perceptual processes that may impact the development of EF and PFC beginning in infancy. We use recent approaches to EF and PFC development as a guide to understanding these individual differences (Amso and Scerif, 2015; Werchan and Amso, 2017).

We propose that caregivers guide attention and early learning through child-directed speech and other forms of social interaction that provide children the opportunity to regulate attention as well as train the PFC to resolve conflict between stimuli with overlapping features beginning very early in development. Child-directed speech and other forms of caregiver interaction (e.g., facial displays, tactile stimulation) direct children's attention to the external environment and stimulate associative learning (Cooper and Aslin, 1990; Kaplan et al., 1996; Werker and McLeod, 1989) and may enhance the neural representations of these stimuli (Gazzaley et al., 2005). These types of caregiver interactions require children to regulate attention and promote learning that facilitates the development of semantic knowledge of perceptually similar stimuli (Chang et al., 2015; Rowe and Goldin-Meadow, 2009; Thiessen et al., 2005). Critically, we argue that this social scaffolding also provides children the opportunity to resolve conflict between multisensory stimuli with overlapping features beginning very early in development. This process in turn supports increasingly complex computations in the PFC as visual processing systems develop and project more complex information to the PFC. We posit that cognitive control develops, in part, through the need to regulate attention to and resolve conflict between such stimuli. Finally, we propose that this early regulation of attention lays the groundwork for the more complex computations necessary for EF that the PFC performs as the child develops (Fig. 1).

These arguments rest on recent approaches to EF and PFC development beginning in infancy. Amso and Scerif (2015) have argued that executive attention processes over visual inputs may be emergent from the functional development of downstream visual systems, in particular through existing feedforward and feedback connections. Visual input from the dorsal and ventral visual pathways converges onto PFC (Gilbert and Li, 2013) in a manner that results in increasing demand on PFC computations to adapt as various visual processing systems strengthen with development. Moreover, the PFC computations that facilitate the early ability to resolve competing perceptual inputs are likely to be similar to those that underlie more complex EF abilities—including working memory, task switching, and inhibitory control—that develop as the PFC adapts to increasingly changing and complex environmental inputs (Werchan and Amso, 2017). Indeed, recent work provides evidence that the PFC is performing computations similar to those of adults in infancy, but is adapted to infants' unique ecological niche (Werchan and Amso, 2017; Werchan et al., 2015).

Expanding on these accounts of early PFC development, we posit that the early regulation of attention and/or resolution of conflict that is facilitated by early interactions with caregivers lays the groundwork for the more complex computations necessary for EF that the PFC performs as the child develops. Through this lens, we describe the mechanisms that might link the quantity and quality of early caregiver interactions and the richness of sensory experience with individual differences in the development of EF and the PFC. We then evaluate this model by presenting evidence in support of hypotheses that fall within this framework and highlight the need for future studies to evaluate hypotheses that remain untested.

In this section, we outline the specific types of environmental experiences afforded by early interaction with caregivers—including cognitive and perceptual stimulation and language processing—that we argue are critical for the development of the PFC and EF abilities. Specifically, we outline two unique pathways through which caregiver interactions and linguistic experience shape early PFC development.

3.1. Attention Regulation Pathway

Unlike sensory systems, the PFC does not receive input directly from the external environment, but rather integrates information from other brain regions, including sensory areas. Amso and Scerif (2015) posit that in typical development, the PFC relies on sensory input and complexity to develop. Early in development, children experience an influx of sensory and linguistic information, and we argue that caregivers play a critical role in guiding children's attention to relevant environmental stimuli in ways that foster the development of EF. Although sensory inputs of many kinds are important in this process, we use the development of the visual system to make our arguments.

Visual information reaches the PFC through projections from both the dorsal and ventral visual cortical pathways (Gilbert and Li, 2013; Kravitz et al., 2013). The dorsal visual stream processes motion and spatial information and encompasses parietal spatial attention systems. The ventral visual stream is critical for object recognition and is made up of regions that respond preferentially to specific types of complex visual categories. These include visual features such as line orientation and color, as well as complex shapes, faces, places, and whole objects (Grill-Spector and Weiner, 2014; Konkle & Caramazza, 2017). The dorsal and ventral streams have both feedforward projections into PFC and receive input through feedback connections from PFC (Gilbert and Li, 2013; Kravitz et al., 2013). While the development of both dorsal and ventral visual pathways is likely important for PFC development (Amso and Scerif, 2015), we focus here on the idea that ventral visual stream circuits might be more susceptible to differences in individual variability in SES and may in turn be particularly relevant to understanding SES/PFC effects highlighted earlier. In particular, the ventral visual pathway processes information that: (1) is learned through interaction with social partners (e.g., faces), (2) is labeled by caregivers through speech (e.g., colors, objects, people, places); and (3) varies in quantity and quality as a function of caregiver ability to provide children with complex sensory stimuli (e.g., toys, books, etc.). We further argue that information coming from ventral visual stream regions provide some of the earliest inputs to the PFC that require complex computations.

Infants are bombarded on a daily basis with novel sensory information, and social interactions with caregivers highlight which of the competing environmental inputs to select (i.e., direct attention to) and which to suppress. One experience through which this happens involves the regulation of attention, for example through child-directed speech (Carpenter et al., 1998; Corkum and Moore, 1998; Mundy and Gomes, 1998; de V. Rader and Zukow-Goldring, 2012,2015; Suanda et al., 2016) and joint attention (Carpenter et al., 1998; Corkum and Moore, 1998; Mundy and Gomes, 1998). Child-directed speech is characterized by a higher pitch and greater pitch range than other types of speech (Kuhl et al., 1997) and often is accompanied by exaggerated facial expressions (Chong et al., 2003). Children prefer speech with these properties, and these unique acoustic characteristics have been shown to direct children's attention to different visual information in the environment (Cooper and Aslin, 1990; Golinkoff et al., 2015; Kaplan et al., 1996; Segal and Newman, 2015; Suttora et al., 2017; Werker and McLeod, 1989). Moreover, infants show increased PFC activity in response to child-directed speech but not adult-directed speech (Peter et al., 2016; Santesso et al., 2007; Zangl and Mills, 2007). For example, caregivers highlight important aspects of children's complex visual world both by drawing their attention to cues the caregiver wants to highlight and by engaging with aspects of the environment in which the child is engaged and helping them pull important features out of a background of visual complexity. This action may in turn increase that particular object's representation in ventral visual stream, which has inputs into the PFC. This guidance by caregivers increases demand on attentional resources to process the information that is being highlighted by the caregiver.

We propose that in environments with limited caregiver interactions, children are given less external guidance to regulate attention and have less experiences involving competition between sensory inputs for attention that must be resolved. This reduced caregiver interaction coupled with reduced access to sensory complexity (e.g., reduced access to books, toys, and complex stimuli with which to engage) may result in limited organized feed-forward information from the ventral visual stream to the PFC. Over development, this may result in lasting differences in PFC functioning and EF abilities.

3.2. Linguistic Pathway

The second pathway through which caregiver interactions may influence the development of EF and PFC is by guiding the recognition and discrimination of objects and people through the acquisition of language and semantic knowledge, a second set of computations that involve feed-forward and feed-backward information streams between the ventral visual stream and the PFC (Gilbert and Sigman, 2007; Serre et al., 2007). The perceptual environment is rich with stimuli with similar features and children must learn to disambiguate, organize, and categorize these stimuli. Recent work shows that the PFC is involved in this process as early as 8 months of age (Werchan et al., 2015).

The complex sensory world generates conflict between stimuli with similar features that needs to be resolved, and semantic tags for these stimuli can help to resolve this conflict. For example, a red ball and a red apple are perceptually quite similar. Through child-directed speech, caregivers help children not only to guide their attention to relevant information in the environment, but also to associate these perceptually similar visual inputs with semantic tags (e.g. red ball with a stem is an apple, red ball without a stem is a toy). When a child is confronted with an object with competition between potential semantic tags (e.g., ball / toy; apple/fruit) in conjunction with input from a caregiver as in the above example, we posit that this provides an opportunity for information to be fed from the ventral visual stream to the PFC to resolve the competition. Children are able to form object category labels via child-directed speech even before they can produce speech (Ferguson and Waxman, 2016), demonstrating that the formation of semantic categories occurs very early in development. The PFC is involved not only in the detection and resolution of competition (Miller and Cohen, 2001), but also in the selection of information from semantic memory when competing alternatives exist (Thompson-Schill et al., 1997). As children learn language, which facilitates object recognition and semantic knowledge, the PFC is continually engaged in the resolution of these types of conflicts and is performing the types of computations that will later be necessary for engagement in more complex forms of competition resolution that are typically considered in the domain of EF (e.g., between competing rule sets and goals).

In the remainder of the paper, we present several key hypotheses that fit within this conceptual framework of the developmental mechanisms linking SES with EF, including: a) SES is associated with cognitive stimulation; b) cognitive stimulation is associated with EF and PFC development; c) SES influences development of the ventral visual stream—potentially more so than the dorsal visual stream—and SES-related differences in cognitive stimulation may explain these differences in ventral visual stream development; d) development of the ventral visual stream scaffolds PFC development and EF; and e) that these associations exist across the entire SES distribution. There is empirical evidence in support of some of these hypotheses, while others remain to be investigated thoroughly. We end by putting out a call for future studies that would directly address all aspects of this conceptual model.

4. Socio-economic status and cognitive stimulation

Below, we evaluate the hypothesis that youths growing up in economically disadvantaged households tend to experience lower levels of cognitive stimulation, including language exposure, caregiver interactions and environmental complexity. Many studies have demonstrated that environmental complexity varies as a function of SES. In seminal work on this topic, Bradley and Corwyn (2002) demonstrated that environmental complexity varies as a function of SES including both income and parental education such that children growing up in higher SES families live in more cognitively stimulating environments. This includes access to enriching experiences (e.g. going to the museum) and educational information (e.g. books), greater parental involvement in learning (e.g. parent teaching child letters and numbers), and greater visual complexity of the home (Bradley and Corwyn, 2002). This finding has been replicated in numerous studies (e.g. Hackman et al., 2015; Hackman et al., 2009; Rosen et al., 2018; Rosen et al., In Press). These findings demonstrate that SES is associated with differences in cognitive stimulation and environmental complexity including access to learning materials, parental involvement in learning, and even visual complexity of the home.

Furthermore, it is well established that the quantity and quality of children's language experience varies meaningfully with SES. In foundational work, Hart and Risley (1995) documented large SES-related differences in the number of words to which children are exposed in the first four years of life. More recent research suggests that both the quantity and quality of language varies by SES and influences language development in children (Gilkerson et al., 2017; Hurtado et al., 2008; Romeo et al., 2018; Rowe, 2012; Weisleder and Fernald, 2013). Language exposure early in development facilitates object recognition by allowing children to learn labels for objects in their environment. This language exposure lays the groundwork for receptive and expressive vocabulary in children. SES is also positively associated with these language abilities (Dickinson and Tabors, 2001; Ramey and Ramey, 2004). Among low-income families, children of parents who use more complex language exhibit greater gains in verbal abilities over time (Hirsh-Pasek et al., 2015). Moreover, SES is associated with differences in children's conversational experience (Hagen et al., 2019), which in turn predict language ability and neural processing of language (Romeo et al., 2018). Additionally, parental verbal scaffolding is associated with SES such that higher-SES parents provide more verbal scaffolding support for their children (Lengua et al., 2007, 2014; Mermelshtine, 2017). This potentially provides structure for the development of attention regulation, which may in turn lay the groundwork for development of higher-level cognitive functions as we discuss below.

5. Cognitive stimulation and executive function

In this section, we present evidence regarding the hypothesis that cognitive stimulation in the context of caregiver interactions supports both EF and neural development. We discuss how variation in cognitive stimulation, caregiver interactions, and linguistic experiences early in development is associated with individual differences in EF and review some evidence that cognitive stimulation is linked to structure and function of both the ventral visual stream and PFC.

Several studies have investigated the associations between cognitive stimulation and EF. Exposure to enriching activities and environmental complexity are associated with child EF, including working memory, inhibitory control, and cognitive flexibility (Sarsour et al., 2012). The degree of cognitive stimulation in the early home environment as reported by caregivers predicts individual differences in children's working memory and planning later in development (Hackman et al., 2015). Recent work from our laboratory replicates and extends these findings to show that cognitive stimulation—assessed with a gold-standard observational measure—is associated with individual differences in working memory, inhibitory control, and cognitive flexibility as well as growth in inhibitory control and cognitive flexibility in early childhood (Rosen et al., In Press). Indeed, in a randomized control trial in Pakistan, an intervention that targeted and improved cognitive stimulation in the home environment was associated with gains in EF skills over time, and this effect was stronger than that of a nutrition intervention (Yousafzai et al., 2016). Moreover, caregiver involvement in learning, including scaffolding, supports the development of EF (Bibok et al., 2009, for review see Fay-Stammbach et al., 2014). Parental scaffolding in early childhood predicts later EF ability (Hammond et al., 2012), and EF mediates the association between parental scaffolding and later academic ability (Devine et al., 2016). Parental scaffolding is associated with EF development over and above the effect of children's cognitive abilities and family SES (Matte-Gagné and Bernier, 2011).

The linguistic environment is clearly important for supporting child language ability and brain systems that support language function, including the PFC (Fernald et al., 2013; Hart and Risley, 1995; Romeo et al., 2018). Recent work suggests that exposure to language also impacts other cognitive abilities including EF and function of the PFC (Sheridan et al., 2012; Hagen et al., 2019). Recent work also provides support for the link between parental language input and child EF ability. For example, Daneri and colleagues found that maternal language complexity and vocabulary diversity were associated with child EF later in development (Daneri et al., 2018). Indeed, recent evidence suggests that children's language abilities are predictive of EF and self-regulation skills (Ayoub et al., 2011; Kuhn et al., 2016). Furthermore, family language complexity, but not child language ability, has been found to be associated with differences in PFC function during complex EF task in 8–12 year olds (Sheridan et al., 2012). Together these findings indicate that the quantity and quality of language exposure along with cognitive stimulation and parental involvement in child learning aid in the development of EF in children.

Links between cognitive stimulation and EF are well documented in children who experience extreme forms of caregiver deprivation, such as early institutional care and neglect. Children exposed to this type of severe caregiver deprivation exhibit difficulty with multiple EF processes, including working memory, inhibitory control, and cognitive flexibility as compared to children reared in families (Bos, 2009; Colvert et al., 2008; Hostinar et al., 2012; Loman et al., 2013; McDermott et al., 2013; Tibu et al., 2016). Additionally, children raised in institutions exhibit differential recruitment of the dorsolateral prefrontal cortex and anterior cingulate while performing EF tasks compared to controls (Mueller et al., 2010).

Together, these studies show that the degree of cognitive stimulation in the early environment, shaped largely through children's interactions with caregivers, are meaningfully associated with EF as well as development of the PFC. This association exists in extreme cases of deprivation, as in the case of early institutional rearing, as well as in more common forms of variation in the home environment across the SES distribution.

6. a SES, cognitive stimulation, and ventral visual stream development

The proposed model suggests that SES should be associated with structure and function of the ventral visual stream, which is explained by SES-related differences in cognitive stimulation.

With regard to the first prediction, meaningful SES-related differences in neural structure have been found in the ventral visual stream in many studies. Specifically, lower income, parental education, and qualifying for free or reduced lunch are all associated with decreased cortical thickness in the ventral visual stream (Mackey et al., 2015; Noble et al., 2015; Piccolo et al., 2016). Additionally, SES is positively associated with recruitment of the fusiform gyrus during working memory for faces and greater recruitment of this region predicts better working memory performance (Rosen et al., 2018).

With regard to the second prediction, we argue that these SES-related differences in both structure and function of the ventral visual stream may be explained by SES-related differences in caregiver interactions, cognitive stimulation, and early linguistic experiences. To our knowledge, there has only been one longitudinal study to date that has investigated how early cognitive stimulation is related to brain structure. Critically, the only regions that show an association between early cognitive stimulation and cortical thickness are the PFC and the ventral visual stream. Results of that study reveal that cognitive stimulation at age four was associated with reduced cortical thickness in the ventral temporal cortex, including the fusiform gyrus, and the prefrontal cortex in late adolescence (Avants et al., 2015). This study shows both specificity of the type of environmental factor and timing of exposure in shaping ventral visual stream and PFC structure: only cognitive stimulation (and not parental nurturance) at age four (but not age eight) was associated with cortical structure in adolescence.

Indirect evidence for a role of cognitive stimulation in shaping visual attention comes from a study of institutional rearing, demonstrating blunted P100 responses—an ERP component involved in perceptual processing—to faces in children raised in deprived orphanages; this early blunted neural response to faces was associated with attention problems later in development, even if the child was removed from the deprived environment before the age of 24 months (Slopen et al., 2012). These findings are consistent with the idea that caregiver interactions shape the development of visual attention and other high-order aspects of visual processing (e.g., object and face recognition). Of course, institutional rearing is an extreme environment. However, coupled with the evidence above describing more normative environments, these findings are consistent with the idea that differences in high-level visual processing are evident in extreme forms of caregiver deprivation as well. Together these findings suggest that both SES and cognitive stimulation early in development may influence the structure and function of the ventral visual stream.

Numerous studied have demonstrated disrupted structure of the corpus callosum, particularly in the splenium, in children who have experienced early life institutionalization (Bick et al., 2015, 2017; Sheridan et al., 2012) or neglect (Teicher et al., 2004). This includes both smaller volume of the splenium (Sheridan et al., 2012) and reduced surface area (Teicher et al., 2004) and white matter integrity (Bick et al., 2015, 2017) of the corpus callosum among those exposed to early-life deprivation. Similarly, higher childhood SES is associated with greater white matter in the splenium in adulthood (Takeuchi et al., 2018). Animal tracing studies show that the splenium, the posterior portion of the corpus collosum, contains fibers that connect extrastriate cortex (Innocenti, 1986; Clarke and Zaidel, 1994; Clarke, 2003) and human diffusion tensor imaging (DTI) studies have found that inferior-anterior portion of the splenium contains fibers from ventral visual stream regions (Putnam et al., 2010). One possibility is that the lack of cognitive stimulation influences not only the cortical structure and function of the ventral visual stream regions, but also impacts the connectivity between these regions.

6. b SES-Related differences in the ventral versus dorsal visual streams

Although reciprocal connections exist between the PFC and both the ventral and dorsal visual streams, existing evidence supports the notion that variation in environmental experience is associated with development of the ventral visual stream and associated functions (see Table 1). For example, a series of recent behavioral studies suggest that SES influences ventral visual stream-dependent processes, including object-based attention (Amso et al., 2014), but not dorsal visual stream-dependent processes, including spatial attention (Markant et al., 2016). Furthermore, SES is positively associated with both feature-based attention for color and object-based attention, processes that are dependent on ventral visual stream function; in contrast, SES is unrelated to attention to motion, which is processed in the dorsal visual stream (Werchan et al., 2019) and disparities in focused attention between high- and low-SES infants emerge as object complexity increases (Clearfield and Jedd, 2012). In addition, numerous studies have demonstrated SES-related differences in both structure and function of the ventral visual stream (Mackey et al., 2015; Noble et al., 2015; Piccolo et al., 2016; Rosen et al., 2018). A recent study found that cognitive simulation early in development predicts differences in cortical thickness in the PFC and ventral visual stream, but not the dorsal stream, in adolescence (Avants et al., 2015). Together these findings provide support for the idea that variation in SES and cognitive stimulation is associated with development of the ventral visual stream and associated functions.

However, it is also possible that the dorsal stream is similarly susceptible to variation in environmental inputs including cognitive stimulation. For example, child-directed speech could drive development of the dorsal stream by impacting orienting of attention and eye gaze, functions that are supported by the dorsal visual stream. Indeed, some studies have found SES-related differences in functional recruitment of the intraparietal sulcus (IPS), located in the dorsal visual stream, during a working memory task (Finn et al., 2016). Furthermore, a study from our laboratory found that cognitive stimulation is associated with cortical thickness in the left IPS (Rosen et al., 2018) and some studies demonstrate SES-related differences in structure of the IPS (Noble et al., 2015). These findings raise the possibility that cognitive stimulation may influence development of both the ventral and dorsal streams which may in turn impact the development of PFC and associated EFs.

7. Development of the ventral visual stream scaffolds PFC development and EF

To our knowledge, no direct evidence exists to demonstrate that development of the ventral visual stream early in childhood scaffolds the development of the PFC and EF. However, in this section we review

Table 1
Evidence from previous studies linking SES and cognitive stimulation with structure and function of the ventral and dorsal visual streams.

Author	Year	Type	N	Age Range	Ventral Stream Evidence	Dorsal Stream Evidence
Amso, Haas, & Markant	2014	Behavioral	72	4 - 14 months	Higher income is associated with greater attentional orienting to faces in infancy	N/A
Markant, Ackerman, Nussenbaum, & Amso	2016	Behavioral	136	9-months	Higher SES was associated with better recognition memory for abstract objects	Higher SES was not associated with spatial attention skill
Werchan, Lynn, Kirkham, & Amso	2019	Behavioral	48	3- to 5-months	Higher SES was associated with a greater ability to engage in color feature-based attention and object-based attention. Associations were linear with SES and not restricted to low SES.	SES was not associated with differences in attention to motion, a process associated with the dorsal visual stream
Clearfield & Jedd	2013	Behavioral	32	6, 9 and 12 months (tested longitudinally)	As the number and complexity of stimuli increased, infants from a higher SES background showed increases in focused attention while infants from lower SES, indicating that lower SES infants did not modulate attention on the basis of stimulus complexity	N/A
Mackey et al.	2015	Structural MRI	58	13-15 years	SES was positively associated with cortical thickness in large swaths of ventral temporal cortex. Greater cortical thickness in the lateral occipital cortex corresponded with higher academic achievement	No significant associations between SES and cortical thickness in the dorsal visual stream.
Finn et al.	2016	Functional MRI	67	13-15 years	Greater activation in ventral temporal cortex and lateral prefrontal cortex among higher income children during a high working memory load was associated with higher math achievement.	During a high load working memory task, SES was positively associated with greater recruitment of the the intraparietal sulcus / superior parietal lobule and middle frontal gyrus
Noble et al.	2015	Structural MRI	1099	3-20 years	Family SES was associated with higher cortical surface area in a large swath of the ventral temporal cortex	Family SES was associated with greater cortical surface area in the intraparietal sulcus
Piccolo et al.	2016	Structural MRI	1099	3-20 years	The left fusiform gyrus demonstrated an SES x age-squared interaction such that low SES individuals demonstrate more rapid cortical thinning across development compared to high SES individuals	No significant associations between SES and cortical thickness in the dorsal visual stream
Rosen et al.	2018	Functional and structural MRI	49	8-16 years	SES is positively associated with recruitment of fusiform gyrus and PFC in a working memory task for faces and recruitment of these regions explains SES-related differences in working memory performance and academic achievement.	Cognitive stimulation is positively associated with cortical thickness in the left middle frontal gyrus and left intraparietal sulcus in children and adolescence.
Avants et al.	2015	Structural MRI	52	18-20 years	Cognitive stimulation at age 4, but not 8, is associated with greater cortical thickness in the ventral temporal cortex and PFC at age 19	No associations between cognitive stimulation and dorsal visual stream structure

existing evidence that is consistent with the idea that development of the ventral visual stream influences development of the PFC and EF (Amso and Scerif, 2015). First, accumulating evidence suggests that functional changes in the ventral visual stream across development play an important role in the development of higher order cognitive function among children. Specifically, activation in ventral visual stream regions (e.g., fusiform gyrus in response to faces; lateral occipital cortex in response to objects) during stimulus encoding and maintenance contributes to improvements in working memory across age (Chai et al., 2010; Rosen et al., 2017; Wendelken et al., 2011). Activation in parahippocampal gyrus and fusiform gyrus during working memory for scenes and faces, respectively, increases with age and is positively associated with both working memory and long-term memory performance (Chai et al., 2010; Rosen et al., 2017, 2018; Wendelken et al., 2011; Fandakova et al., 2019). Together these findings suggest that ventral visual stream development may play an important role in supporting EF performance and memory across development. Second, it is well-established that structural maturation of the PFC is protracted and that occipital, temporal, and parietal cortex maturation precede that of the PFC (Gogtay and Giedd, 2004; Sowell, 2004). Additionally, reciprocal feedforward and feedback connections exist between the PFC and both dorsal and ventral visual streams (Gilbert and Li, 2013; Kravitz et al., 2013).

It has been proposed that the earlier development of more posterior regions including the ventral and dorsal visual streams helps support development of the PFC by feeding the PFC information about the environment (Amso and Scerif, 2015). Experience-dependent differences in environmental inputs including sensory complexity and caregiver interactions may then impact these reciprocal connections. However, it is clear that additional studies are needed to directly test both the idea that development of ventral visual stream function scaffolds development of PFC function and that variation in cognitive stimulation influences these processes.

8. Variation in cognitive stimulation, EF, and PFC structure and function across the entire SES distribution

In this section, we provide support for the hypothesis that variation in cognitive stimulation, language exposure, EF, and PFC structure and function spans the entire SES distribution and are not simply present at the lowest end of the spectrum. The association between SES and EF exists along the entire distribution, such that even among wealthy families there is a positive association between SES and EF (Amso and Lynn, 2017; Hackman et al., 2015; Lengua et al., 2014; Noble et al., 2007; Rosen et al., 2018; Sarsour et al., 2012). SES is also associated with cognitive stimulation and parental scaffolding along the entire SES distribution (Bradley et al., 2001; Carr and Pike, 2012; Hackman et al., 2015; Rosen et al., 2019; Sarsour et al., 2012; Yunus and Dahlan, 2013). Similarly, differences in language quantity and quality also exist across the entire SES spectrum (Cartmill et al., 2013; Fernald et al., 2013; Gilkerson et al., 2017; Hart and Risley, 1995; Schwab and Lew-Williams, 2016). A recent study suggests that variation in cognitive stimulation predict variation in EF even at the high end of the SES distribution (Amso et al., 2019). Growing evidence also documents SES-related differences in neural structure and function, including in the PFC and ventral visual stream (Rosen et al., 2018; Finn et al., 2016; Noble et al., 2015). Importantly, studies that have looked at SES as a continuous variable have found that SES-differences in neural structure and function are present along the entire SES distribution (Noble et al., 2015; Rosen et al., 2018; Ursache and Noble, 2016). Moreover, studies have demonstrated that cognitive stimulation, parental involvement in learning, and parental language complexity mediate the association of SES with EF (Hackman et al., 2015; Sarsour et al., 2012; Sheridan et al., 2012; Daneiri et al., 2018; Rosen et al., 2018; Rosen et al., In Press). Thus, variation in cognitive stimulation, language experiences, and the frequency and quality of caregiver interactions are reasonable candidate mechanisms explaining why SES-related differences in EF and PFC structure and function exist along the entire distribution.

9. Future directions

This piece provides a novel conceptual framework from which to launch future research. Here, we discuss important questions that require further investigation. First, the data that we present here are for the most part cross-sectional and correlational. We advance the idea that cognitive stimulation drives development of the ventral visual stream which communicates through feedfoward-feedback loops to drive development of the PFC and related EFs. However, due to the lack of longitudinal imaging and behavioral data, these data are also consistent with the reverse idea: that the development of the PFC and related EFs drive the development of the ventral visual stream. In order to disentangle these possibilities, future longitudinal work should demonstrate that development of regions of the ventral visual stream and related sensory processes precedes and predicts both EF performance and PFC structure and function.

Relatedly, the timing of this sensitivity is poorly understood. Some work points to the importance of cognitive stimulation early in development being associated with EF and brain structure later in childhood and adolescence (e.g. Slopen et al., 2012; Avants et al., 2015), but without longitudinal studies starting in infancy, understanding the window of sensitivity is impossible. Understanding the timing of sensitivity to these inputs is critical to designing effective interventions to improve EF. Moreover, experimental intervention studies are needed to determine a causal link between cognitive stimulation and development of the ventral visual stream, PFC, and EF. Indeed, recent work found that an intervention designed to increase cognitive stimulation improved EF in children (Yousafzai et al., 2016), but whether such an intervention would directly impact the ventral visual stream and in turn the PFC is unknown. Importantly, the ventral visual stream becomes specialized starting in infancy (Nelson, 2001; Pascalis et al., 2002) and matures relatively early in childhood (Grill-Spector et al., 2008; Scherf et al., 2007). If PFC development relies on early interactions with the ventral visual stream, some sensitive periods for PFC development may be earlier than typically thought.

Our focus here is on how individual variability relevant to SES may shape the ventral visual stream, and in doing so, may impact the development of the PFC. We support our conceptual model with numerous studies that have highlighted SES-related differences in structure and function of these regions (Mackey et al., 2015; Noble et al., 2015; Piccolo et al., 2016; Rosen et al., 2018), and evidence that these regions are impacted by cognitive stimulation early in development (Avants et al., 2015). Some evidence suggests that SES and cognitive stimulation may also be associated with structural and functional differences in the dorsal visual stream including the superior parietal lobule and intraparietal sulcus (Finn et al., 2016; Rosen et al., 2018). It is possible that cognitive stimulation similarly impacts development of the dorsal stream, which may in turn influence development of the PFC. Future studies should directly test the associations of SES and cognitive stimulation with patterns of behavior that are supported by the ventral (e.g., object-based attention) and dorsal (e.g., spatial attention) visual stream as well as patterns of neural function and connectivity with the PFC within the same sample. It will also be important for future longitudinal research to examine how patterns of neural function and connectivity in the dorsal and ventral visual streams influence later PFC development.

Furthermore, we argue that caregiver interactions coupled with an environment rich with sensory information help support PFC and EF development. We believe that both of these aspects of the environment are critical. For instance, simply having access to toys that teach numbers without the presence of a caregiver to help guide learning may not lead to strong EF development. However, whether each of these aspects of cognitive stimulation is equally important and whether their impact is additive remains unknown and requires a more nuanced assessment of the home environment in future studies. Additonally, it remains unknown how specific types of caregiver interactions (e.g. parental language complexity vs. parental scaffolding) might impact EF and neural development differently. Our hypothesis is that both quantity and quality of caregiver interactions are critical. We predict that any environment that reduces a child's ability to receive consistent and reliable information from caregivers to guide attention and learning would impact development of EF, the ventral visual stream and PFC structure and function. Future work should measure caregiver interactions using a wide variety of dimensions (e.g. stimulation-deprivation, safety-threat, predictable-unpredictable) to disentangle the precise elements of parenting that are most strongly related to neurocognitive development.

Our current model posits that higher levels of cognitive stimulation drive development of EF in children. However, it is also possible that these associations reflect either genetically-mediated pathways or that children with higher EF abilities elicit more cognitive stimulation from their caregivers. With regards to the first, parental cognition is also positively associated with child neurocognitive development, which could reflect genetic influences on cognitive development and that higher maternal cognition is associated with greater engagement in scaffolding and other behavior that stimulates cognitive development in children (Bacharach and Baumeister, 1998; Hanscombe et al., 2012). There is considerable controversy regarding whether SES moderates the genetic influences on intelligence such that the environment accounts for a greater proportion of the variance among low SES children while genetic factors play a greater role among high SES individuals (Figlio et al., 2017; Tucker-Drob and Bates, 2016; Turkheimer et al., 2003; Hanscombe et al., 2012). A recent twin study that investigated the role of the home environment in the relations between genetic factors, SES, and intelligence found that the association between genetics and child IQ is stable across the SES distribution, while environmental factors are more strongly associated with IQ in low-SES children compared to their high-SES counterparts (Hanscombe et al., 2012). Interestingly, the magnitude of the association of the home environment—including cognitive stimulation and parental engagement—with child cognitive outcomes is stronger than the associations of both SES and maternal IQ with cognitive outcomes (Tong et al., 2007). Moreover, parental scaffolding of child learning mediates the association between SES and cognitive development in children, even after controlling for maternal cognition (Ronfani et al., 2015). Thus, existing evidence suggests that although parental cognitive ability plays a role in children's cognitive development, the quality of the home environment—including the degree of cognitive stimulation—plays an important role in cognitive development over and above these effects. Thus, it is possible that interventions designed to increase cognitive stimulation in the home may be effective in improving cognitive and neural outcomes in children regardless of the cognitive abilities of caregivers.

With regard to reverse causation, children with greater cognitive abilities may engage in more conversation, exhibit greater interest in learning, ask more questions, and exhibit faster learning than children with lower abilities. Indeed, several longitudinal studies suggest that children with greater cognitive abilities elicit greater stimulation from parents over time (Tucker-Drob and Harden, 2012; Lugo-Gil and Tamis-LeMonda, 2008). However, in a recent longitudinal study from our laboratory, cognitive stimulation predicted growth in EF over an 18-month delay in early childhood whereas EF did not predict growth in cognitive stimulation (Rosen et al., In Press). Although these associations are clearly reciprocal, we focus on the pathway from cognitive stimulation to EF as it presents a clear and modifiable target for interventions aimed at improving cognitive development.

Finally, children raised in low SES environments are at risk for experiencing numerous adverse outcomes, including substance abuse, psychopathology, and lower levels of academic achievement (Patrick et al., 2012; Baydar et al., 1993; Brooks-Gunn and Duncan, 1997). Future research is needed to evaluate whether altered neural development in the ventral visual stream and PFC contributes to these outcomes. Interestingly, adolescents with altered recruitment of the PFC and ventral visual stream during inhibitory control and working memory tasks are more likely to go on to use alcohol and other drugs later in adolescence (Norman et al., 2011; Squeglia et al., 2012; Tervo-Clemmens et al., 2019). Additionally, SES-related differences in recruitment of the fusiform cortex and PFC during a working memory task for faces was positively associated with academic achievement (Rosen et al., 2018). It is possible that altered neural development in these circuits plays a role in the wide range of adverse outcomes observed among children raised in low-SES environments. Greater research is needed to identify the neural mechanisms contributing to these disparities.

10. Conclusion

We propose a novel mechanistic account of how the early environment scaffolds the development of EF as well as PFC structure and function. Specifically, we propose that cognitive stimulation—which encompasses access to a complex environment with developmentally appropriate learning materials, a rich variety of experiences, a complex linguistic environment, and the presence of a caregiver who interacts with the child consistently and uses strategies that promote learning—is critical in shaping the development of EF and the PFC and explains disparities in EF among children raised in lower-SES households. In this paper, we propose that cognitive stimulation early in development helps to shape PFC development by providing opportunities to regulate attention and resolve conflict between competing visual inputs, including through input from the ventral visual pathway, which may in turn produce enhanced representation of visual stimuli. We further argue that language exposure supports the development of EF by supporting object disambiguation and semantic knowledge. We provide evidence that these pathways are a plausible mechanism linking early environmental experience to the development of EF and the PFC. Specifically, we demonstrate that SES is associated with cognitive stimulation and that variation in cognitive stimulation is associated with individual differences in EF and the structure and function of the PFC. Furthermore, we review evidence that SES and cognitive stimulation are associated with structure and function of the ventral visual stream and that cognitive stimulation varies across the entire SES distribution and can explain the presence of SES-related differences in EF and PFC even in high-SES families. We suggest that these differences in experience beginning early in development may produce lasting differences in development of visual association cortex which in turn impacts development of PFC circuitry and EF. Studies that aim to test this biologically plausible model have potential to uncover the environmental and neural mechanisms underlying SES-related disparities in EF as well as the developmental windows in which children are most sensitive to cognitive stimulation. This work will be important for determining the types of interventions that may be most effective for mitigating SES-related disparities in cognitive and academic outcomes.

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