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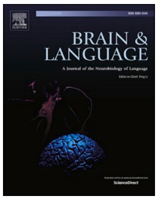

Towards a model of language neurobiology in early development

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ABSTRACT

Understanding language neurobiology in early childhood is essential for characterizing the developmental structural and functional changes that lead to the mature adult language network. In the last two decades, the field of language neurodevelopment has received increasing attention, particularly given the rapid advances in the implementation of neuroimaging techniques and analytic approaches that allow detailed investigations into the developing brain across a variety of cognitive domains. These methodological and analytical advances hold the promise of developing early markers of language outcomes that allow diagnosis and clinical interventions at the earliest stages of development. Here, we argue that findings in language neurobiology need to be integrated within an approach that captures the dynamic nature and inherent variability that characterizes the developing brain and the interplay between behavior and (structural and functional) neural patterns. Accordingly, we describe a framework for understanding language neurobiology in early development, which minimally requires an explicit characterization of the following core domains: i) *computations* underlying language learning mechanisms, ii) *developmental patterns of change* across neural and behavioral measures, iii) *environmental variables* that reinforce language learning (e.g., the social context), and iv) *brain maturational constraints* for optimal neural plasticity, which determine the infant's sensitivity to learning from the environment. We discuss each of these domains in the context of recent behavioral and neuroimaging findings and consider the need for quantitatively modeling two main sources of variation: individual differences or *trait*-like patterns of variation and within-subject differences or *state*-like patterns of variation. The goal is to enable models that allow prediction of language outcomes from neural measures that take into account these two types of variation. Finally, we examine how future methodological approaches would benefit from the inclusion of more ecologically valid paradigms that complement and allow generalization of traditional controlled laboratory methods.

1. Introduction

Infants and toddlers acquire language at a rapid pace, with little apparent effort, and achieve most language milestones by age three. Infants are indeed better language learners than adults and, in a matter of months, can learn complex features of their native language(s) regardless of culture, family background and language topology. Typically developing children master the phonetic contrasts of their native language(s) by the end of their first year. They begin to form their first form-to-meaning mappings at approximately 6 months of age and produce their first words at the one-year mark. Soon after, their vocabulary grows rapidly and, by the end of their second year, children can produce multi-word utterances and engage in conversations. During these early years, the brain is particularly malleable and responsive to experience and substantial changes are observed across both brain structure and function. Despite these unique developmental feats, most research on language neurobiology has focused on the mature adult brain. Partly, this is due to the unique challenges posed by pediatric neuroimaging and the limited availability of experimental methodologies and analytic pipelines that allow careful studies of age-related changes and infant-to-adult comparisons (Barkovich, Li, Desikan, Barkovich, & Xu, 2019; Cusack, McCuaig, & Linke, 2018; Raschle et al., 2012). Importantly, the infant brain undergoes rapid developmental changes that affect brain structure, metabolism, and function. Precise modeling of these dynamic neural patterns requires age-appropriate experimental protocols, as well as pre- and post-processing techniques that are tailored to the needs of pediatric populations, such as methods that deal with motion artifacts and high-water content (Silbereis, Pochareddy, Zhu, Li, & Sestan, 2016;

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Vasung et al., 2019).

Our understanding of brain structure and function has considerably improved since the early studies on language neurobiology by physicians Paul Broca and Karl Wernicke, which paved the way to the first neurobiological models of adult language processing. Several non-invasive neuroimaging methodologies (e.g., fMRI, MEG, EEG, fNIRS) are currently available to conduct investigations of language neurobiology in early development. Furthermore, robust approaches for reducing motion artifacts (Grayson & Fair, 2017; Power, Schlaggar, & Petersen, 2015; Yan et al., 2013) and methodological protocols for conducting pediatric neuroimaging studies (Ellis et al., 2020; Greene, Black, & Schlaggar, 2016; Turesky, Vanderauwera, & Gaab, 2021) have been developed in the last decade. In the context of these advances, we consider here the fundamental elements that are necessary to obtain a comprehensive model of language neurobiology in the developing brain. Understanding language neurodevelopment is crucial to answer fundamental questions such as the impact of experience on brain development and function, or how the maturational timing of different brain structures interact with the language input and the changing computational infrastructure underlying language learning. Furthermore, infant neuroimaging can contribute to the creation of models that predict developmental trajectories, which has the potential to allow identification of language delays and/or disorders before the emergence of behavioral symptoms and thereby enable clinical interventions when they may yield the greatest benefits.

The goal of this review is to provide a framework for understanding language neurodevelopment that captures the dynamic nature of the language learning process. Language, and human cognition more generally, emerges from complex patterns of neural activity, which unfold across sets of distributed structural and functional networks (Byrge, Sporns, & Smith, 2014; Smith & Thelen, 2003; Smith, Byrge, & Sporns, 2020). These patterns of neural activity drive real-time behaviors, and in turn, these behaviors and interactions with the environment evoke specific neural patterns, which change brain connectivity. Understanding the interplay between behavior and neural activity is crucial to delineate neurodevelopmental trajectories . The dynamic patterns of language neurodevelopment can be observed across at least four domains: i) underlying computations that allow children to extract structure from the input, ii) longitudinal behavioral and neural measures, iii) age-dependent environmental and social cues that support language learning, and iv) brain maturational constraints across both structure and function, which determine optimal neural plasticity. The framework presented herein aims to provide a review of these four core domains, with a particular focus on language neurodevelopment, and aims to go beyond identification of *when* certain language-relevant neurobehavioral changes develop. The ultimate goal of this framework is to build neurodevelopmental trajectories of language learning that capture the impact of experience, the social context, environmental stimuli and maturational constraints in supporting and fine-tuning aspects of language learning across neural and behavioral measures.

The manuscript is structured as follows. We first provide a description of the framework and its main components with examples drawn from prior literature. Second, we discuss how this framework will necessitate quantification of both trait (i.e., between-subjects) and state (i.e., within-subjects) patterns of neural and behavioral variation across development. Next, we consider how quantification of neuro-behavioral variation may in turn enable prediction of language measures from neural patterns, which opens the door for developing robust neural and behavioral markers of language outcomes that are relevant for early diagnosis of speech and language disorders. The manuscript ends with some timely reflections about how the implementation of more ecologically valid paradigms, in combination with theoretically grounded observations, may improve the generalization of findings to real-life contexts.

2. A framework for understanding language neurobiology in early development

Investigations into the neural mechanisms subserving language functions have focused primarily on the adult brain. The Wernicke-Lichtheim-Geschwind ‘classical model’ of language processing was the first model proposed to capture how the adult brain processes linguistic stimuli (Broca, 1861; Geschwind, 1965; Lichtheim, 1885; Wernicke, 1874). This model relies on single-word processing and deficit-lesion associations in stroke patients. It proposes an interplay between a left inferior frontal region (Broca’s area) assumed to support language production and a posterior temporal brain area (Wernicke’s area), claimed to subserve language comprehension. These areas are structurally connected by the arcuate fasciculus fiber bundle. Despite its simplicity (or maybe because of it), the Wernicke-Lichtheim-Geschwind model has dominated the field of language neurobiology and influenced clinical assessments of speech, language and reading disorders, even to this date. Over the last two decades, research on language neurobiology has undergone a paradigmatic shift thanks to the advent of non-invasive functional brain imaging, which has increased the spatial and temporal resolutions with which investigations into language neurobiology can be conducted. For example, cytoarchitectural and immunocytochemical data have shown that the canonical Broca’s area is composed of at least 10 subregions, which may implicate a larger number of functions than previously assumed (Amunts et al., 2010). Language-relevant areas extend beyond the classical regions identified in this initial model and include regions in the right hemisphere, as well as subcortical structures thought to play key roles in language processing, such as the cerebellum, the thalamus, and the basal ganglia. The connectivity of these regions is also much more complex than initially proposed and certainly not restricted to the arcuate fasciculus (Fedorenko & Thompson-Schill, 2014). Finally, neuroimaging studies across cognitive domains have revealed that the human brain is organized into several distributed functional networks that interact at multiple spatiotemporal scales (Petersen & Sporns, 2015; Sporns, 2013; Yeo et al., 2011). These findings, along with progress in computational methods and the availability of large-scale neuroimaging datasets, have set the stage for models on the functional neuroanatomy of language that move beyond spatial localization of Brodmann areas to identification of distributed neural networks at both cortical and subcortical levels.

Current models of language neurobiology in the adult brain aim to develop mechanistic and ultimately explanatory hypotheses that link neurobiological mechanisms with computationally explicit psycholinguistic processes. These models increasingly rely on a close connection among disciplines such as neuroscience, cognitive psychology, computational modelling, and linguistics. These inter-disciplinary efforts have led to models of language processing that are theoretically motivated and both neurobiologically and computationally grounded. Although these models differ in the details of the hypothesized computational processes and set of brain regions involved, all of them rely on cortical interactions between a primarily left-lateralized set of regions that includes areas in the prefrontal, temporal and parietal cortices and are connected via ventral and dorsal pathways (Bornkessel-Schlesewsky & Schlesewsky, 2013; Friederici & Gierhan, 2013; Friederici & Wartenburger, 2010; Friederici, 2018; Hagoort, 2017, 2019; Hickok & Poeppel, 2007; Poeppel, 2014; Ullman, 2016). Most of the data contributing to these models come from studies on word retrieval, sentence-level syntax, and semantics. A set of right-lateralized regions including the right temporoparietal junction and the medial prefrontal cortex subserve processing of pragmatic information and processes related to theory of mind and mentalizing.

There are both methodological and analytical challenges that have prevented the elaboration of similar models of language development in the infant and child brain with robust timelines of changes across both behavioral and neural levels. These limitations have been discussed extensively in prior work (Copeland et al., 2021; Cusack et al., 2018;

Dubois et al., 2021; Ellis et al., 2020; Turesky et al., 2021). Here, we focus on identifying the core components that we argue need to be integrated across linguistic domains to achieve a comprehensive understanding of language neurobiology in early development. We will focus on auditory language comprehension and on the first three years of life, an age by which the main language developmental milestones have been achieved and during which most language delays and disorders emerge (Feldman, 2019; Gervain, 2020). Although language modalities vary in the type of input/output (e.g., the oral-auditory modality of spoken languages, the visual-gestural modality of sign languages and the tactile modality of deaf-blind languages), we expect that this overall framework will be relevant for other language modalities as well. To illustrate this framework, we will be drawing on findings from the prior literature within the domains of native-language phonemic discrimination and early lexicon development.

Specifically, we argue that modeling language neurobiology requires an understanding of at least four core domains. First, a description of the *computations* underlying language learning mechanisms (e.g., tracking of statistical regularities from the environment), which will contribute to characterize the types of input that are relevant for extracting linguistic structure. Second, an understanding of how neural and behavioral patterns *change* over time, which will help delineate neurobehavioral trajectories of typical and atypical development. Third, consideration of the types of environmental and *social cues* that reinforce language learning over time, which will shed light on how environmental factors (e.g., caregiver-child interactions) impact the learning process. Fourth, a description of the brain's *maturational trajectories,* which determine optimal neural plasticity and constrain learning from the environmental input. Findings across these four core domains need to be integrated to achieve a comprehensive understanding of language neurobiology in early development.

From a more practical standpoint, this framework can be illustrated by considering the case of a 10-month-old infant who is learning their first word-referent pairings. Some of the questions that this framework aims to address are: What types of input is the infant using to extract linguistic information? How does the learning process impact behavioral and neural activity? How do behavior and neural measures change over time as a function of learning? What are the social and environmental factors that support language learning? Finally, how do brain maturational processes constrain the learning process? Fig. 1 illustrates this framework, which hypothesizes that language-relevant neural patterns depend on a widespread and distributed set of networks that are dynamically evolving across development to support language learning. This set of networks may not be necessarily unique to processing linguistic stimuli and may change as a function of the computations underlying the learning process, the environmental stimuli (including the social environment), and brain maturational constraints. The remainder of this section describes in more detail each of the core domains included in this framework.

2.1. *Computations underlying language learning mechanisms*

Speech processing – extracting meaning from sound-pressure variations – is fast and largely incremental since several levels of linguistic processing (e.g., phonetics, syntax, semantics, prosody) occur in parallel as soon as a single word is heard. How do infants extract structure and meaning from this complex signal that requires rapid form-to-meaning mapping? Specifically, what are the elements in the speech signal that infants use to extract information about language structure and the *computations* (i.e., transformations of the input) that underlie this process? We refer in this section to two types of computations that rely on extracting statistical regularities from the speech input: tracking of transitional probabilities between syllables, which supports segmentation of the speech stream; and tracking of co-occurrence frequencies across words and referents, which supports learning of word-referent pairings.

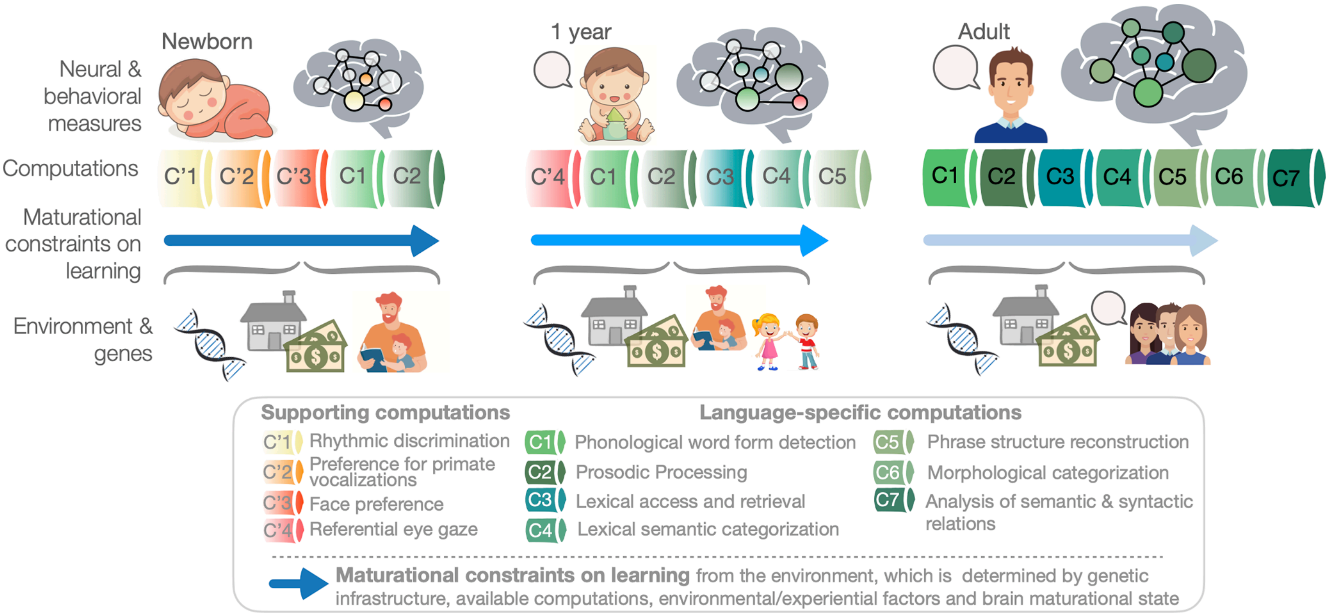

Fig. 1. Schematic illustration of framework and key components to understand language neurobiology in early development. Neurodevelopmental changes are shown for three different developmental stages: newborn, one-year old and adult. A comprehensive account of language neurodevelopment requires an understanding of at least the following components and associated interactions: i) patterns of change across neural and behavioral measures, ii) computations underlying language learning mechanisms, which include language-specific (e.g., phonological word-form detection), as well as supporting (e.g., rhythmic discrimination) computations; iii) maturational constraints on sensitivity to learning from the environment, and iv) genes and environmental variables that reinforce language learning (e.g., face-to-face interactions, socioeconomic status.). *Computations*: Gradient color indicates formation of the computation and solid color indicates that the computation is mature. *Maturational constraints on learning*: Changes in color across developmental stages illustrate age-dependent changes in sensitivity to learning from the environment. Language-specific computations have been adapted from Skeide and Friederici (2016). Environmental variables and supporting computations are representative examples and do not comprehensively capture all possible computations.

2.1.1. *Computations underlying discrimination of native phonemic categories*

To the adult mind, the speech input is a complex signal. This complexity can be illustrated by considering how speech is parsed into meaningful units. At the acoustic level, speech sounds in a given language are grouped into phonetic units, which are the acoustic instantiations of specific articulatory gestures that constitute the consonants and vowels. Importantly, there is substantial variability across phonetic units, and a main task for the learner is to identify the specific phonetic units that constitute the sounds of their native language(s) (Kuhl & Rivera-Gaxiola, 2008; Kuhl, 2007, 2014). This task is particularly challenging because the speech signal does not have any reliable markers to easily identify meaningful units of speech. Furthermore, there are a number of sources of variation that affect the acoustic features of speech sounds. For example, the phoneme /p/ in English can be produced aspirated [p^h] or unaspirated [p]. The surrounding sounds will determine which of these two sounds is ultimately produced. When the /p/ sound appears in word-initial position and followed by a stressed vowel, speakers will choose to produce the aspirated version [p^h], whereas the [p] sound will be preferred in most other contexts. Therefore, although phonetic differences can be observed between these two sounds, they both belong to the same phonemic category in English. Crucially, exchanging these two sounds will never lead to a change in meaning (i.e., they are allophones), unlike in other languages where [p^h] and [p] indicate different word meanings (e.g., Mandarin Chinese). Another source of variability is due to differences across speakers, for example as a result of variation in their speech articulators (e.g., fundamental frequency and speaking rate). Variation can be observed in formant locations, which refer to the concentration of acoustic energy around a given frequency in the speech waveform and that vary as a function of vocal tract shape and tongue position (Kent & Vorperian, 2018). Indeed, variation in the spectra of both vowels and consonants is present even when the same word is repeated by the same speaker (Bürki, 2018; Jacewicz & Fox, 2008).

Despite the inherent variation in the speech signal and the lack of segmentation markers that indicate the boundaries of syllables or words in a phrase or sentence, the mature adult brain efficiently groups speech sounds into the phonemic categories of their native language(s). How does the infant brain learn to categorize speech sounds into the native language categories? Specifically, what are the computations that subserve speech segmentation and therefore early language learning? One type of computation that has been proposed is the ability of infants to accumulate statistical evidence across instances of speech sounds. Evidence for this type of implicit computation was first shown in 8-month-old infants by Saffran, Aslin and Newport (Saffran, Aslin, & Newport, 1996), who used a statistical learning paradigm to show that infants are sensitive to the transitional probabilities between syllables in continuous speech. Specifically, the authors tested whether infants could use transitional probabilities to segment the speech into meaningful (i.e., word-like) units. They exposed infants to a continuous computer synthesized string of coarticulated consonant–vowel syllables (e.g., 'tibudopabikugolatudaropi"). The transitional probabilities were 1.0 among the syllables that made up the pseudo-words included in the string ("tibudo", "pakibu", "golatu", "daropi") and 0.33 between any other adjacent syllables. The speech stream contained no other cues that could potentially supplement the sequential statistics, such as pauses, intonational patterns, stress differences or breaks. Therefore, the only cue to word boundaries was the transitional probabilities that occurred between syllables. Upon familiarization with the string for 2 min, the infants' listening preferences were tested by exposing them to two of the original words and two part-words, which were created by concatenating syllables that crossed word boundaries (e.g., "dopaki", which consists of the last syllable of "tibudo" and the first two syllables of "pakibu"). The infants showed longer listening times for part-words, thus indicating that they discriminated between word and part-word stimuli and therefore had detected the regularities in the original speech stream. Subsequent work showed that infants were indeed tracking transitional probabilities and not simply frequency of test words and part-words (Aslin, Saffran, & Newport, 1998).

This sensitivity to sequential regularities in the input is also crucial for word segmentation and acquisition of phrase structure (Erickson, Thiessen, & Graf Estes, 2014; Estes, Evans, Alibali, & Saffran, 2007; Hay, Pelucchi, Estes, & Saffran, 2011; Saffran et al., 2008; Saffran, 2001, 2002; Shukla, White, & Aslin, 2011). Speech segmentation via accumulation of statistical evidence is indeed essential for word learning since infants use their knowledge of statistical patterns in the input signal to generate new representational units that can be mapped onto meaning (Estes et al., 2007; Lany & Saffran, 2010; Thiessen & Saffran, 2007; Werker, Cohen, Lloyd, Casasola, & Stager, 1998). In other words, they do not only accumulate statistical evidence across instances of speech sounds, but also use this information to map their first sound-to-object meaning associations. There are additional types of computations that are used to build the early lexicon, to which we turn to in the next section.

2.1.2. *Computations underlying early lexicon formation*

Word learning relies on the ability of infants to form word-referent pairings. To succeed, the learner needs to minimize the uncertainty of the referent at the moment when a novel word is encountered. This is a particularly complex task in early word learning since everyday contexts often present highly ambiguous learning environments with multiple potential referents and novel words. Prior studies, however, have shown that infants may benefit from such rich and complex natural learning environments to solve this indeterminacy problem. Specifically, infants seem to rapidly keep track of multiple word-referent co-occurrences and evaluate statistical regularities across individually ambiguous words and scenes in order to build their first word-referent mappings. Smith and Yu (Smith & Yu, 2008) conducted one of the first studies showing that 12- and 14-month-old infants narrow down this hypothesis space by accumulating statistical evidence across ambiguous word-scene pairings. Infants were taught 6 word-referent pairs through a series of *individually* ambiguous trials. On each trial, infants heard two words and were presented with a scene that contained two potential referents. Although the word-referent pairings were ambiguous on each trial, a given word always occurred with its assigned referent across trials. Therefore, tracking co-occurrence frequencies across words and referents could in principle disambiguate the correct word-referent pairs. The results revealed that infants looked longer at the objects more strongly associated with the auditorily presented word forms relative to the more weakly associated forms. These data were the first to show that infants indeed evaluate statistical evidence across individually ambiguous trials to establish word-referent associations and that learning of word-picture associations occurs rapidly (within less than four minutes of exposure).

These statistical learning patterns must be grounded on a theoretical understanding of how cognitive development unfolds over time. For example, tracking of cross-situational statistics to form word-referent mappings may rely on (at least) two different learning mechanisms (Smith & Yu, 2008). The learner might build hypotheses for each specific ambiguous trial, which are either confirmed or disconfirmed by subsequent trials. The outcome of this learning process is a set of confirmed hypotheses that the learner relies on to build word-referent mappings. Alternatively, the learner might accumulate associations between words and referents across trials. These associative links would be strengthened or weakened based on the reliability of word-referent mappings across trials. The outcome of this learning process is a set of stronger correct associations relative to wrong associations for each correct word-referent pair. Providing a theoretical grounding of how these computations unfold may yield an understanding of how non-linguistic cognitive abilities, such as memory or attention, contribute to cognitive development more generally and language learning specifically. Furthermore, neuroimaging data acquired during the learning process may shed light on the potential learning mechanisms underlying these statistical patterns. Although infant studies are currently lacking, recent fMRI data with adults using model-based representational similarity analyses (RSA) have shown that cross-situational learning is more likely mediated by a propose-but-verify (PbV) mechanism. Under the PbV mechanism, only one hypothesis is stored for each word-referent pair and, if confirmed on subsequent trials, it is retained (Berens, Horst, & Bird, 2018). Crucially, the individual does not store additional associations between the word and other potential referents until the initial hypothesis is rejected. This mechanism therefore predicts a rapid change in the neural representations associated with each correct word-object pair. It contrasts with a more gradual change in word-referent neural representations during learning, which would be predicted by associative models in which the learner accumulates word-reference associations that are strengthened or weakened across trials. The authors found evidence for the PbV learning mechanism, which seems to be supported by rapid pattern-separation processes in the hippocampus. The results of the study, however, do not address whether PbV and associative mechanisms operate separately in parallel, as has been advocated by other accounts on cross-situational learning (Kachergis, Yu, & Shiffrin, 2016; Stevens, Gleitman, Trueswell, & Yang, 2016; Yurovsky & Frank, 2015)

In addition to accumulating statistical evidence from the environment, infants rely on certain heuristics that allow them to narrow down their initial hypothesis space, such as a bias to generalize a word to other objects that have the same shape (Carey, 1978; Gleitman, 1990; Markman, 1990) or to associate labels to a whole object rather to a part of the object (Landau, Smith, & Jones, 1992; Smith, Jones, & Landau, 1996). Statistical evidence from the input along with these cognitive biases likely interact to facilitate word-meaning mappings in early development. Importantly, the relevant linguistic and extra-linguistic cues and computations that underlie language learning mechanisms vary across age, which illustrates the dynamic nature of language development.

Infant learners may use multiple cues simultaneously at any point in time to extract information about linguistic regularities. For example, 6-month-olds use information about phrasal prosody (i.e., rhythmic and intonational cues that mark the boundaries between phrases) (Shukla et al., 2011) and their knowledge of function words (de Carvalho, Babineau, Trueswell, Waxman, & Christophe, 2019) to infer the meaning of new words. At approximately two years of age, when they have a fair amount of lexical and grammatical knowledge, toddlers use word order and argument structure to infer the meaning of a novel word and use this knowledge for subsequent comprehension and learning (Naigles, 1996; Yuan & Fisher, 2009). At this age, they are also able to track the semantic relationships between novel words on the basis of their positions within sentences (Wojcik & Saffran, 2015). Therefore, infants and toddlers may not only rely on several basic statistics for language learning (e.g., transitional probabilities or cross-situational statistics), but also on other features of the speech signal (e.g., prosodic patterns or sentence structure), as well as the visual and social contexts (e.g., the objects in view or the speaker's gaze) (He & Arunachalam, 2017; Romberg & Saffran, 2010). Finally, although not discussed here, learners show variation in their abilities to use regularities from the input to identify linguistic structure as a result of their attentional (Toro, Sinnett, & Soto-Faraco, 2005; Turk-Browne, Jungé, & Scholl, 2005) or memory skills (Johnson & Tyler, 2010). Ultimately, identification of the relevant informational units that children rely on to extract linguistic regularities, as well as an explicit description of the underlying computations, will provide the basis for identification of developmental changes in infants' behavior and neural patterns.

2.2. Delineating neural and behavioral trajectories in early language learning

Language learning is a highly dynamic and age-dependent process, which requires an understanding of *patterns of change* in order to delineate potential behavioral and neural trajectories of typical and atypical development. At the behavioral level, developmental timelines associated with the mastery of specific language skills have been clearly established. For example, the "perceptual narrowing" abilities observed in the first year of life or the developmental stages described in the acquisition of the first form-to-meaning mappings are well documented. At the neural level, studies often focus on identification of the "neural correlates" underlying language-related processes at a given age or developmental period. At the structural level, studies have attempted to describe potential developmental trajectories of brain maturation associated with the acquisition of specific linguistic skills (Perani et al., 2011; Skeide & Friederici, 2016). The relationship between these developmental changes and the evolving computational infrastructure that underlies the learning process, however, remains relatively unexplored. In this section, we focus on findings in the domains of phonemic discrimination and word learning that illustrate how developmental changes can be investigated across neural and behavioral levels. We also discuss how the inclusion of neuroimaging methods with higher spatial resolution, including the use of multimodal imaging approaches, can provide a better understanding of neurobehavioral changes in early development.

2.2.1. Developmental changes in discrimination and mastery of phonemic categories

Language skills develop incrementally and the ability to acquire new aspects of language changes over time as a result of the accumulated knowledge and interactions with the surrounding environment. An example of this dynamic developmental process can be observed at the perceptual level as infants learn the sounds of their native language(s) during the first year of life. Discrimination and mastery of phonemic categories in the native language occurs because of the infant's sensitivities to aspects of the environment during what is referred to as a period of "perceptual narrowing". Perceptual narrowing entails a reduction in sensitivity to certain aspects of the environment. These sensitivities are often experience-induced in that they allow "narrowing" of broader knowledge when optimal stimuli are encountered in the environment.

The first studies investigating perceptual narrowing in early development were conducted by Werker and colleagues in the domain of speech perception (Werker, Gilbert, Humphrey, & Tees, 1981; Werker & Tees, 1984). Werker and colleagues (Werker et al., 1981), for example, investigated phoneme discrimination in adult native speakers of either Hindi and English, as well as 7- and 12-month-old infants born to English-speaking parents. The participants were tested in their discrimination of the Hindi voiceless, unaspirated retroflex versus the voiceless unaspirated dental stops (/ʈa/ and /ta/) and the Hindi voiced versus voiced aspirated dental stops (/t^h/ and /d^h/). The results showed that only adult native speakers of Hindi and 7-month-olds were able to discriminate these sounds, whereas adult native speakers of English and 12-month-olds only discriminated the English phonemes. Since then, a number of cross-linguistic studies have shown that infants' perceptual discrimination of speech sounds includes a broader set of distinctions early in development, and over time the set of speech sounds narrows down to include only the contrasting sounds in the native language(s)

(Byers-Heinlein & Fennell, 2014; Flom, 2014; Lewkowicz & Ghazanfar, 2009; Lewkowicz, 2014; Scott, Pascalis, & Nelson, 2007). These developmental changes in speech perception show that infants display sophisticated abilities early in life, some of which do not fully develop due to the lack of exposure to certain types of input. The broader capabilities of the infant brain early in life and its rapid adaptability to environmentally relevant distinctions allow humans to learn rapidly and adapt quickly. These changes therefore reflect a progression towards a more efficient processing of salient environmental input, rather than a developmental regression (Scott et al., 2007). Perceptual narrowing has been observed across a variety of domains and sensory systems, such as infants' perception of faces (Hayden, Bhatt, Joseph, & Tanaka, 2007; Kelly, Liu, et al., 2007; Kelly, Quinn, et al., 2007; Maurer & Werker, 2014; Pascalis et al., 2005; Scott, Pascalis, & Nelson, 2007), music (Hannon & Trehub, 2005) and multisensory auditory-visual perception (Lewkowicz & Ghazanfar, 2009; Lewkowicz, Sowinski, & Place, 2008; Pons, Bosch, & Lewkowicz, 2019). Importantly, these studies go beyond identification of when certain skills or abilities develop by accounting for the impact of experience and environmental stimuli in fine-tuning aspects of language learning across development.

Developmental neural changes in response to speech input have been observed across linguistic domains, although large-scale longitudinal studies in infant language development are currently lacking. The main research questions usually focus on how behavioral patterns are instantiated in the brain at a specific age or developmental period. Most studies in early development have been conducted using recordings of event-related potentials (ERPs), which have high temporal resolution (less than1 ms) and reflect the rapid unfolding of neural events in response to a given stimulus. At the acoustic level, for example, discrimination of phonetic contrasts modulates the mismatch negativity (MMN) component in infants (Dehaene-Lambertz & Pena, 2001; Kuhl & Rivera-Gaxiola, 2008; Rivera-Gaxiola, Silva-Pereyra, & Kuhl, 2005), which had been previously associated in adults with phonetic discrimination (Näätänen et al., 1997). One of the earliest studies was conducted by Kuhl and colleagues (Kuhl & Rivera-Gaxiola, 2008; Kuhl, 2004), who exposed infants at 7.5 months to both native and non-native contrasts and found that variation at the neural level in both native and non-native discrimination predicted language abilities later in life. Better neural discrimination of the native contrast predicted advanced language skills at 24 months in word production and sentence complexity measures, mean length of utterance at 30 months and faster vocabulary growth. In contrast, better neural discrimination of the non-native contrast predicted poorer language skills across the same measures and slower vocabulary growth. Recent studies have found that this process of neural discrimination of phonetic contrasts may be supported early in life by the infant's sensitivity to temporal modulations of speech (i.e., amplitude and frequency modulations) (Bertoncini, Nazzi, Cabrera, & Lorenzi, 2011; Cabrera & Werner, 2017; Cabrera, Bertoncini, & Lorenzi, 2013). Indeed, neonates are already sensitive to these fine-grained details of the speech signal and show similar brain lateralization patterns as in adults (Cabrera & Gervain, 2020). From a developmental standpoint, an interesting question is the extent to which the infant relies on temporal modulation features (e.g., fast and slow amplitude modulations) relative to the amount of exposure to the native language and their ability to identify native versus non-native sounds. Future investigations into the neural basis supporting phonetic discrimination can shed light on how speech input and experience impact brain development and language abilities across age.

2.2.2. *Developmental changes associated with word learning and early lexicon formation*

Another type of developmental change that demonstrates the dynamic nature of the language learning process is observed in the domain of spoken word comprehension. By 5 months, infants respond to their own name and show a preference for their name relative to another word matched in stress pattern (Mandel, Jusczyk, & Pisoni, 1995). They begin to establish the first form-to-meaning mappings between 6 and 9 months, which are often nouns that appear frequently in their environment and that are visually accessible, such as foods or body parts (Bergelson & Aslin, 2017). At approximately 10–13 months, infants begin to learn the meanings of verbs and abstract words, which are less commonly found in their social context and often do not have a visually accessible referent when they are produced by the caregivers (Bergelson & Swingley, 2013b). Crucially, after the first year, infants experience a non-linear increase in their ability to understand words (McMurray, 2007) regardless of the type of stimuli (e.g., still images or videos), part of speech (e.g., nouns or verbs) or familiarity with the stimuli (Bergelson and Swingley, 2013a, 2015, 2018; Bergelson, 2020; Garrison, Baudet, Breitfeld, Aberman, & Bergelson, 2020). The onset of this so-called "comprehension boost" likely requires the maturation of certain cognitive abilities that facilitate language learning, such as joint attention, which allows the child and caregiver to attend to the same object or event; or the ability to use pointing for social interactions and intention sharing (Bergelson, 2020). This substantial improvement in comprehension is also supported by the development of language-related skills, such as the ability to identify and segment meaningful units from the input (Bergelson, 2020). Indeed, children's segmentation skills, specifically the ability to extract statistical structure from the input (e.g., via identification of transitional probabilities between syllables) during the first year of life predicts success in word comprehension and productive vocabulary later in development (Ellis, Borovsky, Elman, & Evans, 2021).

Neuroimaging studies of early word learning have focused largely on the neural correlates of real-time auditory processes. These studies often use electrophysiological measures, specifically ERPs, to determine whether a given ERP component is elicited as the child listens to words. Most studies focus on the period between 12 and 24 months of age, which is when the comprehension boost is observed. Specifically, neural activity in response to familiar versus unfamiliar words has been associated with three components: a left-temporal or fronto-central N200-500 component (Friedrich & Friederici, 2005; Mills, Coffey-Corina, & Neville, 1993, 1997), a centro-parietal N400 component (Mills, Coffey-Corina, & Neville, 1993; Mills, Coffey-Corina and Neville, 1997; Thierry, Vihman, & Roberts, 2003; Kooijman, Hagoort, & Cutler, 2005; Kooijman, 2007; Friedrich and Friederici, 2008, 2011; Torkildsen et al., 2009, for a recent review see Junge, Boumeester, Mills, Paul, & Cosper, 2021), and a broadly distributed N600-1200 component (Mills et al., 1997; Conboy & Mills, 2006). The N200-500 component signals a more negative amplitude within 200-500 ms after word onset for familiar words relative to unfamiliar words. In contrast, the N400 shows a more negative amplitude for familiar relative to unfamiliar words. This N400 effect is already present in 6-month-olds in response to recently acquired word-object mappings, although it shows a slightly later onset than in 12-month-olds (Friedrich & Friederici, 2011). In 3-month-olds, the N400 effect appears to be missing; instead, infants show a late negativity when repeatedly exposed to several novel words paired consistently (or inconsistently) with novel objects, which may be indicative of initial acquisition of lexical regularities (Friedrich et al., 2015). Finally, the N600-1200 effect represents a more negative response for familiar than unfamiliar words and has been associated with early word learning since it is present in 12- to 17-month-olds, but not in 19- to 20-month-olds (Conboy & Mills, 2006; Friedrich & Friederici, 2005; Mills, Coffey-Corina, & Neville, 1997). More recently, involvement of the right frontal cortex in response to familiar (versus unfamiliar) words has also been observed in an MEG study with 14-month-old infants (Bosseler et al., 2021). This right-lateralized effect was found primarily in the middle (400–600 ms) and late (600–900 ms) time windows, which resemble those found in earlier ERP studies. This response seems to be larger for familiar versus unfamiliar words in the right temporal cortex, which is an area that has been associated with form-to-meaning mapping (Hickok & Poeppel, 2007; Skeide & Friederici, 2016). This study additionally found a positive correlation between brain activity in the right frontal cortex and subsequent measures of vocabulary growth at 18, 21, 21, and 27 months.

A main limitation of ERP measures is their limited spatial resolution due to the difficulties of accurately identifying how local field potentials propagate through neural and non-neural tissues to reach the electrodes on the surface of the scalp (Srinivasan & Nunez, 2012). Given that spatial information is essential to achieve an understanding of *how* the human brain processes information, an increasing number of studies are leveraging methodologies that provide higher spatial resolution (e.g., fNIRS, fMRI, MEG), including the use of multimodal-imaging approaches, such as simultaneous data collection of both EEG and fNIRS signals. fNIRS is a non-invasive neuroimaging methodology that provides relatively good spatial resolution of roughly 2 cm (Quaresima & Ferrari, 2019) and therefore can serve as an excellent complement to EEG/ERP studies. Furthermore, simultaneous EEG-fNIRS studies are relatively easy to implement in comparison to other multi-modal imaging approaches (e.g., fNIRS-fMRI, EEG-fMRI) and can be used in both laboratory-controlled contexts and more naturalistic and ecologically valid settings (Aslin, Shukla, & Emberson, 2015). Multi-modal imaging investigations, especially those including longitudinal measures and dense sampling across age, are a promising method to investigate the neural changes that support language learning in early development.

2.3. Social environmental cues that reinforce early language learning

Social interaction and natural language-learning situations (e.g., reading books or playing with toys) critically support language learning (Ferjan Ramírez, Lytle, Fish, & Kuhl, 2019; Kuhl, 2007, 2010, 2014; Li & Jeong, 2020; Lytle, Garcia-Sierra, & Kuhl, 2018; Ramírez-Esparza, García-Sierra, & Kuhl, 2017). Face-to-face interactions facilitate language learning by providing social cues (e.g., referential eye-gaze, facial expressions, gestures) that enhance the infant's attention and emphasize the relevant contextual information. Furthermore, the quantity and quality of the speech input (e.g., number of word tokens, mean length of utterance or diversity of vocabulary), are also associated with vocabulary growth (Fernald & Marchman, 2011; Fernald, Perfors, & Marchman, 2006; Weisleder & Fernald, 2013). Importantly, while most research has been conducted on Western, educated, industrialized, rich and democratic (WEIRD) populations, infants raised in disadvantaged communities show larger variability in language abilities as they face additional challenges that affect child-caregiver interactions and that have implications for school readiness (Fernald, Weber, Galasso, & Ratsifandrihamanana, 2011; Fernald, Marchman, & Weisleder, 2013; Henrich, Heine, & Norenzayan, 2010). We will review some of this evidence in this section.

2.3.1. Face-to-face interactions

Face-to-face communication with a caregiver is inherently multimodal and a number of social cues beyond language are present during communication (e.g., facial expressions, gestures, gaze following). A communicative cue that infants are extremely sensitive to from early in development is eye gaze. A number of studies have shown that eye gaze is an important cue in language development as it enhances language learning across a number of domains such as vocabulary development, form-to-object mapping and speech processing (Brooks & Meltzoff, 2005; Carpenter, Nagell, Tomasello, Butterworth, & Moore, 1998; Morales et al., 2000). Gaze following and eye contact increase attention and arousal mechanisms by emphasizing the relevant information and therefore directing the infant's attention towards it, thus facilitating the child's engagement (Çetinçelik, Rowland, & Snijders, 2021; Yu & Smith, 2017). Furthermore, the child's *sustained* attention, defined as the ability to stabilize visual attention to an object for periods longer than 3 s, rather than *joint* attention per se, is crucial for prediction of future language skills and cognitive development more generally (Kannass & Oakes, 2008; Lawson & Ruff, 2004; Ruff & Lawson, 1990). Indeed, infants who visually attend longer to an object show more robust memory during an object-naming task than those who engage in briefer attention states (Macroy-Higgins & Montemanaro, 2016; Pereira, Smith, & Yu, 2014; Salley, Panneton, & Colombo, 2013; Yu, Suanda, & Smith, 2019).

The developmental trajectory of gaze following as a learning mechanism is characterized by an early phase in which infants show a preference for upright faces with open eyes and specialization of cortical areas associated with processing gaze cues (Carpenter et al., 1998; D'Entremont, Hains, & Muir, 1997; Farroni, Csibra, Simion, & Johnson, 2002; Gredebäck, Fikke, & Melinder, 2010; Perra & Gattis, 2012). Indeed, newborns already show a preference for faces with open eyes versus closed eyes (Batki, Baron-Cohen, Wheelwright, Connellan, & Ahluwalia, 2000) and for upright faces versus inverted faces (Farroni et al., 2002; Farroni, Johnson, & Csibra, 2004). Infants develop the ability to follow the interlocutor's gaze starting at 3 to 4 months of age and gaze-following becomes a stable cue of social communication between 6 and 8 months (D'Entremont et al., 1997; Gredebäck et al., 2010). It is not until 9–12 months of age, however, that eye gaze starts to be used as a referential mechanism and facilitates language learning by providing eye-directed referential information (Brooks & Meltzoff, 2005; Butler, Caron, & Brooks, 2000; Caron, Butler, & Brooks, 2002; Johnson, Ok, & Luo, 2007; Woodward, 2003). The neural correlates of this developmental trajectory have been investigated via ERP measures in 9-month-olds, who already appear to process eye-gaze information in an adult-like fashion (Senju, Johnson, & Csibra, 2006; Striano, Reid, & Hoehl, 2006). This developmental path, however, may be more complex since several other ostensive cues are present in parallel in naturalistic learning settings. How much an infant relies on each of these cues may be determined not only by age, but also by the nature of the task or the complexity of the communicative interaction (Striano, Chen, Cleveland, & Bradshaw, 2006). For example, attention to the mouth also plays a role in language learning as it provides information about the shape of the mouth and speech sounds (Tsang, Atagi, & Johnson, 2018). Attention to the mouth increases in 12-month-old infants when they are exposed to non-native sounds (Lewkowicz & Hansen-Tift, 2012), when they are challenged by a bilingual environment (Pons, Bosch, & Lewkowicz, 2015), or when they are exposed to novel words (Tenenbaum, Sobel, Sheinkopf, Malle, & Morgan, 2015). It is also observed in infants ranging in age between 14- and 18-months, which coincides with the "vocabulary burst" phase (Hillairet de Boisferon, Tift, Minar, & Lewkowicz, 2018). Goubet and colleagues (Goubet, Rochat, Maire-Leblond, & Poss, 2006) have indeed hypothesized that the use of social cues may play less of a role in learning when the infant has already mastered a specific skill or task.

The quantity and quality of the speech input during human interactions are also relevant variables in language learning and have been related to vocabulary growth (Hoff, 2003; Hurtado, Marchman, & Fernald, 2008; Huttenlocher, Waterfall, Vasilyeva, Vevea, & Hedges, 2010; Rowe, 2012). Weisleder and Fernald (Weisleder & Fernald, 2013), for example, showed that the amount of child-directed speech at 19 months predicts real-time processing measures and vocabulary growth at 24 months. Caregivers' vocal responses to babbling with either vowels or words rapidly shapes the infant's vocalizations, and infants begin to incorporate the phonological patterns produced by the caregiver, which promotes the learning of new vocal forms (Goldstein & Schwade, 2008). Furthermore, parent coaching by increasing moments of infant-/child-directed speech and *parentese* speech style (i.e., speech characterized by higher or exaggerated prosody, shorter utterances and enlarged vowel space (Fernald, 1985; Cooper & Aslin, 1990; Pegg, Werker, & McLeod, 1992; Fisher & Tokura, 1996) improves infant babbling between 6 and 14 months and leads to a larger vocabulary at 14 months (Ferjan Ramírez et al., 2019). Gains in the number of utterances and vocabulary size have also been observed in non-Western populations (Weber, Fernald, & Diop, 2017).

Child-caregiver interactions are affected by environmental variables, such as socioeconomic status (SES). Indeed, SES impacts the quality and quantity of the speech input (Hoff, 2003, 2006); for example, children born to lower-SES families often show slower real-time language processing efficiency and slower vocabulary growth than those raised in higher-SES families (Fernald et al., 2013). Families in low SES settings show substantial variability in the number of child-caregiver's interactions, which impacts real-time processing efficiency of familiar words and predicts subsequent expressive vocabulary scores (Weisleder & Fernald, 2013). A number of experiential variables account for the impact of SES on cognitive and social development, among them differences in sanitation, nutrition, access to healthcare, environmental pollution or stress levels (Bradley & Corwyn, 2002). Differences in language learning as a result of SES can emerge as early as 9 months and have been shown to predict later school performance (Halle et al., 2009; Walker, Greenwood, Hart, & Carta, 1994).

Given the relevance of parent–child interactions for language learning, recent neuroimaging studies have begun to investigate how these communicative exchanges impact brain development. Until recently, most neuroimaging research on early social interactions focused on neural patterns in the infant brain in response to a unidirectional social stimulus presented on a screen. These conventional paradigms, however, do not capture the dynamic and bidirectional interactions between the child and the caregiver (Hoehl & Markova, 2018). These neurobehavioral dynamics of child-caregiver interactions can be investigated via "hyperscanning", which refers to the simultaneous data collection of neural activity from more than one person taking part in a social interaction (Montague et al., 2002). For example, the temporal dynamics of social interactions are associated with the temporal alignment of neural oscillations among child and caregiver. Several studies have shown that during a social interaction, neural synchronization occurs as a result of both verbal and non-verbal cues (Dumas, Lachat, Martinerie, Nadel, & George, 2011; Hasson, Ghazanfar, Galantucci, Garrod, & Keysers, 2012). The alignment of neural oscillations to an exogenous stimulus or "entrainment" occurs when child and caregiver achieve similar interpretations for a given input and when there is successful exchange of information (Nguyen, Bánki, Markova, & Hoehl, 2020). Importantly, this shared neural coupling appears when there is a shared "understanding" of a given input, such as a story presented auditorily, and not simply due to the shared exposure to a given stimulus.

One of the few studies implementing a hyperscanning paradigm with infants was recently conducted by Piazza and colleagues (Piazza, Hasenfratz, Hasson, & Lew-Williams, 2020), who used live interactions between infants (9- to 15-months-olds) and adults during a naturalistic two-way interaction that included playing, singing and reading. The results showed that infant-to-adult neural coupling is greater during social interactions with each other relative to an adult-to-adult interaction in which the child was present but did not interact with any of the adults. The study revealed that the adult and infant brains differentially engage with a variety of social cues (e.g., eye gaze, joint attention, speech prosody) as a function of their social importance. For example, prefrontal activation in both the infant and adult brains was significantly coupled to the timecourse of mutual gaze, which suggests that both individuals anticipated joint eye contact. Furthermore, an increase in the infant's prefrontal activity was reliably followed by pitch variability in the adult's speech, which was likely the result of the adult producing extreme pitch contours in response to a range of infant behaviors (e.g., when highlighting a certain word). Altogether, dual-brain studies open new opportunities to study infant development in reciprocal interactions and how infant's learning strategies evolve during the course of natural communication.

2.4. Maturational constraints that support early language learning

Interactions between the genetic infrastructure, which determines the range of abilities that can be expressed, and environmental factors that shape the timing of gene expression – which ultimately code for behavior – play an important role in language neurodevelopment. These evolutionary and experiential influences are present early in development and have been extensively studied in primary sensory systems across species, but they can also be observed in higher-level cognitive systems such as language (Hensch, 2005; Knudsen, 2004). They are evident during developmental periods in which the brain's neural infrastructure is particularly sensitive to structuring and restructuring as a result of exposure to certain types of environmental inputs (Hensch, 2005). The timing of these developmental periods, so-called "sensitive periods", are determined by both the maturation of the underlying neural systems and exposure to certain types of environmental stimuli (for a review on the biological underpinnings of this process, (see Takesian & Hensch, 2013; Werker & Hensch, 2015; Voss, Thomas, Cisneros-Franco, & de Villers-Sidani, 2017; Reh, Hensch, & Werker, 2021).

Sensory systems show the clearest examples of experience-induced brain plasticity early in development. For example, an eye deprived of vision or so-called "lazy" eye shows a long-lasting loss of responsiveness in primary visual cortex (V1). This is the result of competition between the two eyes as they converge onto individual neurons in V1. This loss of connectivity underlying the "lazy" eye leads to poor visual acuity. Research on gene targeting in mice has shown that the *precise timing* at which this ocular dominance occurs can be manipulated by rewiring the functional and structural connectivity that underlies this imbalanced sensory experience (Takesian & Hensch, 2013). This temporal window of plasticity during which the neural infrastructure is reorganized as a result of experience is referred to as "experience-induced" neural plasticity. These windows of neural plasticity are necessary to ensure optimal neural representation of the environment and are thought to be an efficient mechanism to guide subsequent behaviors. Although these adaptive changes occur early in life in response to experience, there is also the possibility of lifelong plasticity for certain experience-induced processes (Werker & Hensch, 2015). The biological mechanisms driving these changes include a series of molecular triggers that interact with the maturation of neuronal circuits (e.g., GABA neurotransmitter) in response to sensory experience to either open a period of neuronal plasticity or consolidate a given neural circuit (for a review, see Takesian & Hensch, 2013; Werker & Hensch, 2015; Voss et al., 2017). The maturation of inhibitory interneurons, specifically fast-spiking parvalbumin-expressing (PV) cells, is a main driver of sensitive periods by regulating plasticity across multiple timescales (Reh et al., 2021; Takesian & Hensch, 2013).

In language development, sensitive periods vary in their timing characteristics as a function of the nature of the linguistic input, such as syntactic (Johnson & Newport, 1989) or phonetic stimuli (Werker & Hensch, 2015) (Fig. 2). Certain language-related systems remain available throughout the lifespan, such as mapping new form-meaning associations (i.e., vocabulary growth) or the ability to adapt to the phonetic properties of native speakers, including accents, which occurs rapidly on a second-by-second basis (Clayards, Tanenhaus, Aslin, & Jacobs, 2008). Sensitive periods in language development have been discussed in greater depth in prior work (Gervain, 2015; Reh et al., 2021; Werker & Gervain, 2013; Werker & Hensch, 2015; Werker & Tees, 2005), so we will limit this section to describe some key findings that provide evidence for both maturational and environmental constraints in language development. The goal is to emphasize the important role of the brain's maturational trajectory and exposure to certain types of experiential input in early life to understand the complex dynamics of language neurodevelopment.

2.4.1. Maturational and experiential factors constraining discrimination of phonemic categories

In language development, the anatomical and functional infrastructure that supports speech processing in the newborn brain already shows similarities to that observed in the adult brain, which suggest that infants are born with a certain "readiness" to process speech signals (Dehaene-Lambertz, Dehaene, & Hertz-Pannier, 2002; Dehaene-

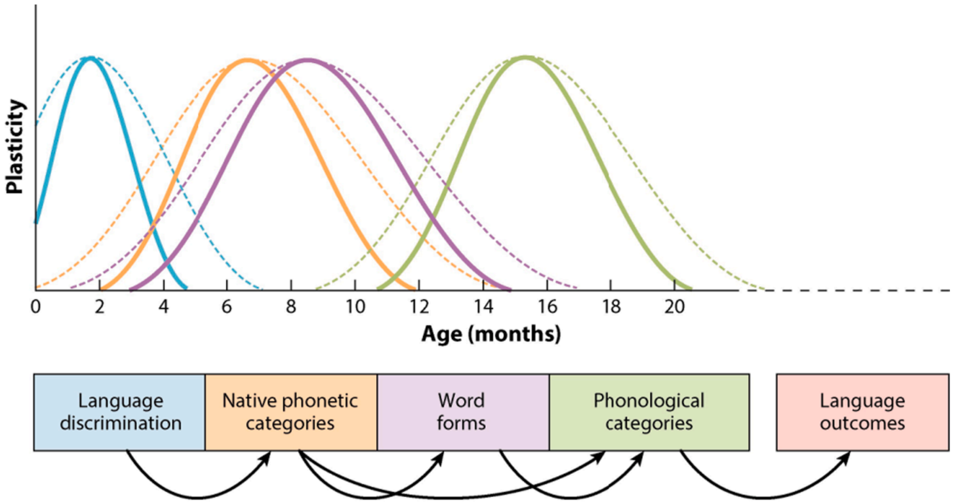

Fig. 2. Illustration of the interacting and overlapping nature of sensitive periods in language development. The curves illustrate sensitive periods associated with the mastery of language skills across four broad categories of developmental milestones. Arrows indicate the cascading and interacting nature of language skills. The opening, peaks, duration, and delays of sensitive periods can by altered by environmental and genetic factors. Reproduced, with permission, from Werker & Hensch, 2015.

Lambertz, Hertz-Pannier, & Dubois, 2006; Peña et al., 2003). Neonates show a preference for speech versus non-speech sounds (Vouloumanos & Werker, 2007) and for cross-linguistic constraints on syllable structure (Gómez et al., 2014). Furthermore, they show differential neural activation when listening to their own native language versus an unfamiliar language (May, Byers-Heinlein, Gervain, & Werker, 2011; Minagawa-Kawai, Cristià, & Dupoux, 2011), likely as a result of prenatal experience with their native language obtained *in utero*.

During the first year of life, infants increasingly adapt their speech sound discrimination abilities to the properties of their native language (Kuhl, Williams, Lacerda, Stevens, & Lindblom, 1992; Mehler et al., 1988; Moon, Cooper, & Fifer, 1993; Werker & Tees, 1984). This process of age-related perceptual attunement or "perceptual narrowing" is constrained by both maturational and experiential factors. Peña and colleagues (Peña, Pittaluga, & Mehler, 2010), for example, showed that infants born 3 months pre-term are not able to distinguish two languages on the basis of their rhythmical characteristics until after 8 months of age. This age corresponds to the gestational age of a 5-month-old full term, which is when within-class rhythmical properties are discriminated in full-term babies. Importantly, this delay is present despite the fact that speech input was available for an additional three months, thus indicating that brain maturational constraints are at play and that experience is not enough by itself to guarantee perceptual attunement to the native language. Furthermore, whereas infants 6–8 months of age are able to discriminate two non-native phonetic categories after exposure to as little as two minutes of these speech stimuli (Maye, Werker, & Gerken, 2002), this flexibility to learn new sounds decreases at approximately 10 months of age. This is the age at which the phonetic inventory of the native language appears to stabilize (Yoshida, Pons, Maye, & Werker, 2010).

Environmental factors that modulate speech experience during early language development also regulate sensitive periods and interact with maturational constraints to accelerate or delay the opening of a given sensitive period. For example, prenatal exposure to an antidepressant (serotonin reuptake inhibitor [SRI]) leads to an acceleration of the perceptual narrowing trajectory. Infants born to mothers who had taken SRI medication during pregnancy fail to discriminate non-native categories at 6 months, which is approximately 4 months earlier than typically developing infants (Weikum, Oberlander, Hensch, & Werker, 2012). Early speech input experiences, such as exposure to two languages, may also lead to a delay in the attunement to the native speech sounds. Some studies suggest that bilingual infants may take longer to master the phonetic categories of the two languages (Bosch & Sebastián-Gallés, 2003) and they remain sensitive during a longer period of time to discrimination of non-native speech sounds (Petitto et al., 2012). Nevertheless, it is important to note that bilinguals ultimately are able to learn the two languages at approximately the same pace, despite the fact that they are exposed to twice the amount of variability in the input and a reduced amount of input to each language (Byers-Heinlein & Fennell, 2014; Costa & Sebastián-Gallés, 2014).

Accumulated experience with speech input and age-related brain maturational constraints undoubtedly interact, thereby necessitating longitudinal studies to define developmental trajectories over time and reveal the impact of experiential and learning constraints. The impact of language experience on learning, especially in the first year of life, is particularly prominent in the case of international adoptions. Individuals who have had early exposure to a first language, in some cases for only a year, still show an advantage in relearning challenging phonemic contrasts from this first language as adults relative to those who never had this early exposure. Importantly, these adults were exposed to a second language most of their lives and often had no conscious recollection of their first language (Choi, Broersma, & Cutler, 2017; Oh, Au, & Jun, 2010; Pierce, Klein, Chen, Delcenserie, & Genesee, 2014; Singh, Liederman, Mierzejewski, & Barnes, 2011).

A recent study by Reh and colleagues (Reh et al., 2021) reveals the complex interaction that exists between brain maturational constraints and experience. The authors investigated whether sensitivity to speech sound discrimination decreases as a function of age when the period of perceptual attunement is closing. They used a cross-sectional design with infants spanning three ages: 5-month, 9-month and 12-month-old infants. This age range captures a continuum that goes from maximal sensitivity to non-native phonemic contrasts and some sensitivity to native sounds (5 months), to an age when infants do not show discrimination of non-native phonemic contrasts and have already established the phonemic repertoire of their native language (12 months) (Choi et al., 2017; Kuhl et al., 2006; Werker & Tees, 1984; Yeung, Chen, & Werker, 2013). The experimental design used EEG to investigate whether infants growing up in a monolingual English environment show differential neural responses during exposure to either a bimodal or unimodal distribution spanning the [r] to [l] phoneme continuum. Critically, these two sounds constitute two distinct native phonemes in English and therefore should be discriminated at all ages. Following familiarization, the test phase required infants to detect a change from /r/ to /l/ (or vice versa) using an oddball paradigm. As expected, exposure to a bimodal distribution led to phoneme discrimination across the three age groups. In contrast, the unimodal distribution led to collapsing of the phonetic category boundaries only at 5- and 9-months of age, whereas the 12-month-old infants continued discriminating the two sounds, which indicates that distributional exposure did not have an effect on phoneme discrimination at this older age. At the neural level, exposure to the unimodal distribution led to a mismatch response to the presentation of the deviant stimuli *only* at 12 months. This study raises the question as to what may underlie the observed decline in the ability to learn from the input at 12 months. One possibility is that the stability of the neural response underlying phoneme discrimination of the two categories /r/ and /l/ interferes with the ability to learn from the speech input after a short distributional exposure (i.e., 2.5 min). A second possibility is that neural plasticity declines with age, which may in turn reduce the sensitivity to learn from the distributional statistics in the input. It seems highly likely that both of these two possibilities interact as they are not mutually exclusive.

Sensitive periods are an excellent illustration of the complex interactions that occur between the maturation of cortical circuits and the effects of experience across development, illustrating the dynamic processes that underlie language neurodevelopment. Collectively, research on brain plasticity and the impact of experiential factors in rewiring neural circuits indicates that there are developmental periods during which the brain is particularly susceptible to learning from environmental stimuli. These temporal windows are relatively malleable in that the amount of experience or variability in the input may delay, accelerate, or broaden certain sensitive periods. The type of input also matters; for example, perceptual development has a more constrained developmental period than other areas of language, such as building new form-to-meaning mappings, which is still possible during adulthood. Recent studies have also questioned the extent to which related factors, such as accumulated knowledge or the potential for plasticity of cortical circuits, may facilitate or interfere with subsequent learning from experience. Future longitudinal studies that span critical developmental windows and manipulate the amount of exposure and type of language input will likely provide answers to these questions.

3. Quantitative modeling of state and trait variation in language neurodevelopment

Characterizing language neurobiology in early development and associated changes across age requires an understanding of how a given child differs from the group-level pattern with respect to neural and behavioral measurements and how children themselves vary over time. In this section, we describe how this goal will necessitate consideration of change observed *within*-individuals (i.e., within-subject differences or state-like patterns of variation) and *between*-individuals (i.e., individual differences or trait-like patterns of variation). Understanding the contribution of, and interactions between, state and trait components of variance will serve as the basis for developing growth curves of both normative and atypical development that enable prediction of language outcomes from neural measurements (Becht & Mills, 2020; Rosenberg, Casey, & Holmes, 2018; Sanchez-Alonso & Aslin, 2020; Telzer et al., 2018; Varoquaux & Poldrack, 2019). In this section, we discuss several sources of within-subject and between-subject variability in early development and consider factors that may impact the reliability of the measurements obtained during periods of rapid change and high variability.

3.1. Trait-dependent (between-subjects) sources of variation in early language development

Characterizing time-dependent relationships across neural and behavioral levels has proven challenging, especially during periods of rapid change. Developmental change is characterized by substantial individual differences at both behavioral and neural levels (Adolph & Robinson, 2011; Adolph, Robinson, Young, & Gill-Alvarez, 2008; Adolph, Hoch, & Cole, 2018; Fenson et al., 1994; Foulkes & Blakemore, 2018; Nelson, 1973). At the behavioral level, the diversity of individual outcomes contrasts with established language “milestones” that aim to describe universal stage-like developmental changes (Feldman, 2019; Misirliyan & Huynh, 2020). Although these milestones and standardized assessment scales have important clinical utility to identify language delays, they do not represent an accurate characterization of individual development since they hide meaningful and considerable variation in developmental trajectories. For example, whereas some infants show signs of understanding words already at 8 months of age and produce their first words before their first year, others do not begin to comprehend and produce speech until their second year (Fenson et al., 1994). Furthermore, some children who are identified as ‘late talkers’ catch up with their peers before school age, whereas others acquire vocabulary more slowly and remain at risk for developmental language disorders (Fenson et al., 1994).

Individual differences in language skills in early development have been associated with children’s early language experiences (e.g., amount and diversity of caregiver’s speech) and cognitive/language stimulation (e.g., caregiver attentiveness and engagement) (Fernald & Marchman, 2011; Hart & Risley, 1995; Hoff, 2003). Indeed, as noted earlier, maternal language input, which is strongly associated with maternal education and socio-economic status (SES), predicts early language skills and subsequent language outcomes (Hoff, 2003; Huttenlocher et al., 2010; Rowe, 2012; Vernon-Feagans, Bratsch-Hines, Reynolds, & Willoughby, 2020). Primary caregivers with a higher-level of education usually have a larger vocabulary with greater lexical diversity and grammatical complexity, more engaging and attentive parenting styles, and have more knowledge of child development, which influences how they verbally interact with children (Bornstein, Haynes, & Painter, 1998; Hoff, 2003; Rowe, 2008). Furthermore, parental education has been found to be strongly associated with neural measures, such as resting-state functional connectivity (FC) in language related areas (Su, Li, Zhou, & Shu, 2021). Among the measures of maternal language input that are related to child language development are the following: total number of words and number of different words, as a measure of lexical diversity; mean length of utterance and number of *wh*-questions, as a measure of grammatical complexity; and number of conversational turns, as a measure of quality of mother–child language interactions (Huttenlocher et al., 2010; Romeo et al., 2018; Rowe, 2012; Vernon-Feagans et al., 2008). There are also substantial age-related differences in the attainment of certain milestones across cultures, such as in vocabulary growth and measures of language processing efficiency (Ertem et al., 2018; Fernald & Marchman, 2011; Fernald et al., 2013; Piantadosi, Jara-Ettinger, & Gibson, 2014), which ultimately affect the timing and rate of vocabulary growth and grammar learning. These cross-cultural differences are the result of differences in language experiences, such as frequency of child-directed speech (Cristia, Dupoux, Gurven, & Stieglitz, 2019; Weber et al., 2017), access to schooling (Cristia et al., 2019) and/or family SES (Fernald et al., 2011; Hammer & Weiss, 1999; Hoff, 2003).

How do these individual differences in language skills at the behavioral level relate to individual differences in neural patterns? A limited number of studies have addressed this question by considering how trait-dependent sources of neural variation in early development relate to differences in language measures that are collected either concurrently or at a later point in development. A recent study by King and colleagues (King, Camacho, Montez, Humphreys, & Gotlib, 2021) investigated how variability in language input relates to fMRI FC patterns (i.e., patterns of covarying spontaneous neuronal activity) of language networks in 5-to-8-month-olds. Variability in FC patterns during resting-state are relatively stable within an individual and therefore can be harnessed to understand how differences in language input during infancy relate to spontaneous patterns of neural activity. The authors recorded 8 hours of naturalistic (i.e., at home) language input using the Linguistic ENvironment Analysis (LENA) device from fifty-one families. The recordings were analyzed with respect to the quantity and consistency of adult words and adult-infant conversational turns. Infants were also scanned during sleep to obtain a measure of their FC patterns among a set of regions of interest that had been previously associated with language comprehension. The results showed that children who engaged in more conversational turns with their caregiver had lower FC in the posterior temporal language network. Although it is still unclear how the strength of FC relates to infant behavior and how to best define language networks in infants, the results of this study provide evidence of how infant-parent interactions can influence the intrinsic functional organization of the infant brain.

In another study, Brito and colleagues (Brito, Fifer, Myers, Elliott, & Noble, 2016) investigated the relationship between language-relevant behavioral and neural variability by asking how trait-dependent sources of neural variation at a given age relate to behavioral variation at *a later point* in development. They collected resting EEG power (i.e., total EEG activity) during sleep in sixty-six full-term neonates and investigated its association with SES, and language and memory skills at 15 months. Although no associations with SES were observed at birth, resting EEG power collected at birth showed positive correlations with memory and language skills at 15 months. Specifically, frontal power was positively correlated with memory scores and parietal power was positively correlated with language comprehension scores. Despite the still limited understanding of how trait-dependent variation in brain function relates to language differences at the individual level in infants and toddlers, these studies are promising as they open the door to understand behaviorally-relevant neural variation in early development. Furthermore, these studies illustrate how the relationship between neural and behavioral variability can be investigated with respect to variation in the child's language skills, but also with respect to variation in the environment (i.e., speech input and caregiver engagement).

3.2. State-dependent (within-subject) sources of variation in early language development

Developmental periods of enhanced within-subject variability are common in early development across both behavioral and neural patterns of activity. Behaviorally, skill acquisition does not follow a step function, but rather it is characterized by the stochastic presence/absence of a given skill until a behavior stabilizes and the new skill is expressed daily (Adolph & Robinson, 2011; Adolph et al., 2008; Adolph et al., 2018; Hadders-Algra, 2018). For example, a child may produce a word one day, but not another (Brown, 1973), and s/he may show increased variability in vocal-articulator movement during the acquisition of new phonetic units, which decreases over time (Grigos, 2009). Periods of stability (i.e., low variability) and periods of transition (i.e., high variability) often alternate over the course of learning (Adolph & Robinson, 2011; Goldin-Meadow, Alibali, & Church, 1993; Siegler, 2006). The variable expression of a given behavior may last for several days, weeks or months (Adolph et al., 2018). Importantly, the appearance of a given behavior often initiates a cascade of developmental processes because the emergence of new skills depends on the development of others (Siegler, 2006; Smith, Jayaraman, Clerkin, & Yu, 2018). The ability to use eye gaze as a referential mechanism, for example, enhances vocabulary growth and contributes to word learning (Brooks and Meltzoff, 2005, 2008; Carpenter et al., 1998; Morales et al., 2000). Production of the first words depends on the ability to segment the speech signal, the development of the vocal articulatory apparatus, and memory improvements among other factors. Consequently, any developmental timepoint cannot be considered in isolation, but rather as part of a dynamic cascade of subject-specific inter-dependent events (Adolph et al., 2018; Siegler, 2007).

Within-subject variability in neural patterns is also expected since the brain undergoes dramatic changes due to maturation in both anatomy and function in early development (e.g., changes in cortical folding patterns, synaptic pruning and restructuring of neural circuits) (Cusack et al., 2018; Grayson & Fair, 2017; Keunen, Counsell, & Benders, 2017). Cognitively relevant neural variability has often been investigated by assessing neural activity as the child is exposed to (at least) two different types of linguistic and/or social stimuli. This traditional approach has been productive, especially when control conditions are included, and measures of neural variation are directly related to language measures collected concurrently or at a later age. Nevertheless, interpretation of neural differences in the absence of behavioral measures is otherwise challenging since it requires *a priori* assumptions about the underlying psychological processes.

Recent studies aim to relate neural variability during specific cognitive tasks with variability in language skills, speech input and/or environmental variables. As an example, Liu and colleagues (Liu et al., 2020) collected fMRI data during natural sleep in 9-month-old infants that were either at high (HR) or low familiar risk (LR) for autism spectrum disorder (ASD). Infants passively listened to three speech streams that differed in the degree to which they contained statistical and prosodic cues to word boundaries (i.e., strong statistical and prosodic cues, strong statistical cues only, or minimal statistical cues). Compared to HR infants, LR infants showed greater activity in the left amygdala and left temporal regions for the speech stream that contained strong statistical and prosodic cues. LR infants also showed increased functional connectivity between the bilateral primary auditory cortex and right anterior insula for this same speech stream. Crucially, greater activity was positively correlated with language skills at 36 months across both groups and it was associated with less severe ASD symptoms in HR infants. The results of this study also serve to illustrate that although state- and trait-dependent sources of variance are orthogonal to each other and therefore can be quantified independently, these two components of variance can be observed concurrently. In other words, a given neural or behavioral variable can simultaneously exhibit within-subject and between-subject change (for a review, see (Sanchez-Alonso & Aslin, 2020). In this case, a given neural measurement (i.e., BOLD activation or FC) can be modulated by both ASD symptomatology and language-related learning cues. Therefore, particularly in neurodevelopmental research, it is essential to investigate the extent to which subject-level variations in neural patterns are stable within a person and/or exhibit state-related change as a function of age or cognitive task.

Within-subject measures of neural variability have also been associated with age-related developmental changes and language skills. Emerson and colleagues (Emerson, Gao, & Lin, 2016), for example, studied the development of primary language regions during the first 2 years of life using fMRI data collected longitudinally during natural sleep. Their results showed that a transition to left-hemispheric asymmetry occurred at ~ 11.5 months of age. At the same age, functional connectivity among language-related regions (inferior frontal gyrus [IFG] and superior temporal gyrus [STG]) increased in the left hemisphere. They also observed an association between the developmental trajectory of the IFG and expressive/receptive language skills assessed using the Mullen Scales of Early Learning (Mullen, 1995) at 4 years of age. Finally, although not much attention has been paid in infant research to moment-to-moment variability during a given testing session (e.g., during story-listening or movie-watching tasks), considering state and trait relationships during a given experimental session can shed light on how brain function reconfigures itself at the scale of seconds to minutes (Betzel, Byrge, Esfahlani, & Kennedy, 2019; Bolton, Jochaut, Giraud, & Van De Ville, 2019; Simony et al., 2016). Future studies that measure moment-to-moment variability can be particularly useful to investigate how learning evolves in real-time and how brain function adapts to experience (Bassett & Mattar, 2017; Bassett et al., 2011; Braun et al., 2015; Waschke, Kloosterman, Obleser, & Garrett, 2021).

3.3. Reliability and reproducibility of state and trait measurements in neurodevelopmental research

Periods of rapid within- and between-subject variability pose challenges to the reliability and validity of neural and behavioral measurements and therefore to identification and interpretation of age-related normative trajectories (Sanchez-Alonso & Aslin, 2020). The reliability of the measurement, specifically, how consistent a given measurement is across repeated tests or sessions over time, will depend on statistical power (i.e., the amount of data necessary in a given session or test to avoid measurement error). For example, length of language samples affects the reliability of measurements that are commonly used to diagnose language impairments (e.g., total number of words, number of different words or mean length of utterance). A common recommendation is to collect 50–100 utterances, which takes approximately 10–15 min (Miller, Andriacchi, & Nockerts, 2015; Paul & Norbury, 2012), although it is unclear to what extent this criterion generalizes across age and data collection procedures (Casby, 2011; Cole, Mills, & Dale, 1989; Darley & Moll, 1960; Minifie, Darley, & Sherman, 1963; Rondal & Defays, 1978). For 3-year-olds, samples of 7–10 min are often sufficient to generate reliable measures (Guo & Eisenberg, 2015). Relatedly, in neuroimaging studies, an important consideration is the impact of scan length on individual-level estimates, which often require longer scanning times relative to group-mean estimates. To reliably identify single-subject neural patterns during resting-state paradigms, it is often recommended that scanning times longer than 25 min are obtained from adults (Anderson, Ferguson, Lopez-Larson, & Yurgelun-Todd, 2011). These scan time requirements are often challenging to meet in developmental studies because infants and young children are often unwilling or unable to lie motionless in the scanner during long scan sessions (Sanchez-Alonso & Aslin, 2020; Vanderwal, Eilbott, & Castellanos, 2019). The reliability of task-based paradigms to estimate individual differences between subjects also increases as a function of scan length (Gordon et al., 2017; Shah, Cramer, Ferguson, Birn, & Anderson, 2016). Data quantity is therefore an important consideration in developmental studies to ensure the reliability of the effects, and requirements may vary as a function of age and data collection method.

The reliability of the measurement is also affected by repeated sampling over time, especially if a given subject is only tested at a few timepoints. Sparse sampling makes it challenging to separate within-subject time-dependent sampling error and spurious sources of within-subject biological variables (e.g., diurnal rhythms or metabolic states) from true age-dependent change as a result of experience or brain maturation. Dense repeated sampling and longitudinal designs are therefore essential to distinguish meaningful within-subject variation from measurement noise, especially during periods of rapid change in which enhanced variability is expected (Adolph & Robinson, 2011). Dense sampling is also necessary to accurately characterize developmental change given that growth is not continuous, but it is rather characterized by a variable expression of a given behavior (Siegler, 2006). Most neuroimaging studies with infants, however, are often conducted at a single age (either at birth or prior to 12 months), which limits our understanding of developmental changes that occur month-to-month during the first year. Similarly, neurodevelopmental changes between the first to second year of life remain understudied (Azhari et al., 2020).

Finally, a related consideration is sample size, which will affect the reproducibility of the effect since small sample sizes often have large variability in estimates, which may lead to model overfitting (Gelman, 2010; Ioannidis, 2008; Yarkoni & Westfall, 2017). Large-scale consortium-level datasets may avoid mistakenly fitting sample-specific noise as true signal. Collectively, these data collection requirements (i.e., large sample sizes, data quantity considerations, longitudinal designs, and dense repeated sampling with short intervals) may be difficult to meet in neurodevelopmental studies but are necessary to ultimately understand the shape and rate of developmental trajectories. Nevertheless, contributions from studies that employ smaller sample sizes and focus on a single-age, cross-sectional comparisons, or longitudinal studies with sparse sampling also play a crucial role in laying the necessary foundation to devote time and resources to large-scale data collection efforts. These more limited studies can contribute to the overall goal by fine-tuning neuroimaging paradigms for a given age range and establishing developmental time points that can be used as a reference to identify periods of stability and enhanced variability in large-scale data collection efforts (Tsui, Marchman, & Frank, 2019).

4. Early markers of language outcomes and clinical applications

Characterizing typical language neurobiology in early development is crucial for early identification of clinical disorders. Speech and language delays in young children can negatively impact critical skills such a reading, writing, attention, and social interactions, and therefore affect later educational outcomes (McLaughlin, 2011). For example, language delays between 2 and 5 years of age have been associated with poor reading skills in elementary school (Catts, Fey, Tomblin, & Zhang, 2002; Durand, Loe, Yeatman, & Feldman, 2013). If these delays persist after age 5, there is increased difficulty in the development of attention and socialization skills (McLaughlin, 2011; Snowling, Bishop, Stothard, Chipchase, & Kaplan, 2006). Most language delays are identified through parental surveillance or during child-well visits when a given developmental milestone is not present, such as delays in speech onset or syntactic difficulties. As a result of this “watchful waiting” approach, most children are identified as having a language delay or disorder by the time they are 2 or 3 years old. At the time of diagnosis, the child’s language skills may be compounded by negative experiential effects because of developing atypically within their sub-optimal social and physical environment for several years. Furthermore, by age 3, key neurodevelopmental events that subserve language behavior have already occurred, thus missing the opportunity for early detection and clinical intervention. Here, we consider an alternative to this approach, namely the development of early markers of language outcomes that can identify speech/language delays and disorders early enough to ensure that clinical interventions provide the greatest benefits. Furthermore, we argue that discovery of neural markers that may allow identification of language outcomes *before* the emergence of behavioral manifestations holds great promise of providing a pathway for early identification of language neurodevelopmental disorders (Fig. 3).

Diagnosis of speech and language delays are commonly based on comparisons with developmental milestones that are expected in typical language development (Schum, 2007). A language delay requires clinical attention when a child’s developmental rate falls below 75% of the expected rate; for example, when a milestone that is expected at 24 months of age is not present in a 30-month-old child (Feldman, 2019). A

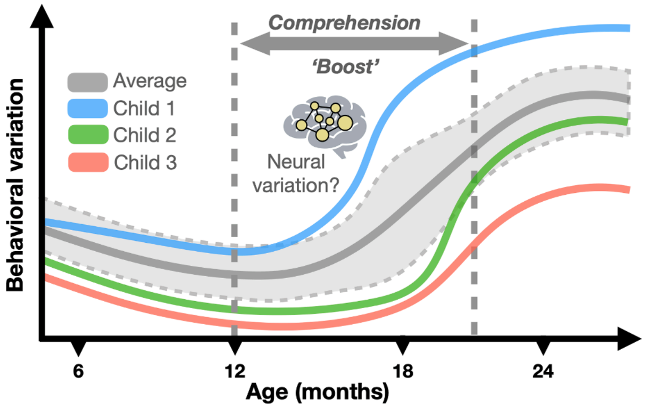

Fig. 3. Identification of neural markers to predict language outcomes before the emergence of behavioral symptoms. Three potential developmental trajectories in word comprehension abilities between 6 and 24 months are shown, as well at the population average. The hypothesized trajectories describe non-continuous growth with variable expression of the behavior (i.e., presence and absence of a given skill) until it stabilizes. Patterns of state (i.e., within-subject) and trait (i.e., between-subject) variation at the behavioral level can be leveraged to identify key neurodevelopmental windows of maximal variation (e.g., the comprehension boost). It is still unkown how neural variation maps onto these behavioral developmental trajectories. Biomarker research before windows of maximal state and trait variation may be particularly relevant to understand early differences in neural patterns before the emergence of behavioral manifestations.

comprehensive evaluation is then performed to assess whether the delayed developmental pattern(s) may be related to a primary language disorder or a secondary developmental disorder, such as autism spectrum disorder (ASD) or global developmental delay (GDD). Children with a language delay follow a typical developmental pattern, but at a slower rate than expected, and may continue to experience difficulties in certain language domains in comparison to their peers who did not experience a delay (Rescorla, 2009). In contrast, children with a language disorder tend to show a different pattern of development that can be characterized by persistent and severe delays in the acquisition of language skills (e.g., syntactic difficulties in children with specific language impairment), developmental regressions (e.g., loss of words between 15 and 21 months in ASD) or impairments in two or more developmental domains (e.g., language and motor function impairments in GDD) (Schum, 2007; Tager-Flusberg, Paul, & Lord, 2005; Zengin-Akkuş, Çelen-Yoldaş, Kurtipek, & Özmert, 2018).

Importantly, there are no agreed upon recommendations regarding screening for speech and language impairments. The first indications of a developmental delay often occur because of parent's concern or during routine well-child visits, except in cases when the child has a comorbid disability that also affects language skills (O'Hare & Bremner, 2016; Schum, 2007). Most language delays are reported after 2 years of age, when children are expected to start combining words, and the absence of combinatorial speech is often the first indication of a developmental delay (McLaughlin, 2011; Rosenbaum & Simon, 2016). Approximately 15% of toddlers are diagnosed as "late talkers", who are defined as children whose vocabulary between 24 and 30 months includes fewer than 50 words and who show no combinatorial speech (Rescorla, 2013). Whereas some children catch up with their peers before school age, 7% of children enter school with long-lasting impairments in language development (Tomblin et al., 1997). This "watchful waiting" approach to diagnose speech and language delays is problematic because by the time a child is diagnosed with a speech or language delay, the child may already be between 2-to-5 years of age. Importantly, speech processing starts already *in utero* and the first two years of life are characterized by the acquisition of critical language-comprehension skills, such as the emergence of the first form-to-meaning mappings at 6 months and the mastery of native sound discrimination between 6 and 12 months of age. As a result, speech therapists and pediatricians often miss critical early developmental windows in which the infant brain is more malleable and plastic in response to experience and during which implementation of clinical interventions can provide the greatest benefits.

An alternative to the watchful waiting approach is to obtain behavioral and neural biomarkers that allow early identification of developmental delays. Biomarkers provide objective indications of a clinical state that can be measured accurately and reproducibly (Strimbu & Tavel, 2010), and that can contribute to the early identification of atypical behavioral or neural patterns associated with a later clinical disorder. For example, a pattern of neural responses at 10 months may serve as an early predictive biomarker of socio-pragmatic difficulties at a later age. Biomarkers leverage the heterogeneity observed in language outcomes and serve as developmental measures that are predictive of later atypical developmental patterns. Although biomarker research in language developmental disorders is still in its early stages, recent findings in language development have identified behavioral and neural measures in early development that can be used to predict subsequent language outcomes. For example, measures of real-time processing efficiency are a potential promising tool for identification of late talkers who will be more likely to catch up versus those who experience a continued delay, especially when used in combination with measures of vocabulary growth. Fernald and Marchman (Fernald & Marchman, 2011) found that speed and accuracy measures in a familiar word recognition task at 18 months predict variation in vocabulary development (i.e., rate and acceleration) from 18 to 30 months of age in both typically developing children and late talkers. This technique also allowed identification of late talkers that were more likely to undergo a more accelerated vocabulary growth over the next year. Furthermore, speed of processing efficiency at 18 months in children born preterm also predicts unique variance (12–31%) in school-relevant measures (i.e., receptive vocabulary, global language abilities and non-verbal intelligence [IQ]) at 4.5 years (Marchman et al., 2018). Similarly, in infants at high-risk for specific language impairment (SLI), rapid auditory discrimination of tone sequences at 7 months is a predictor of language development in subsequent outcome measures at 12, 16, 24 and 36 months of age. At 36 months, this auditory measure along with sex explains 40% of the variance in language outcomes (Benasich & Tallal, 2002).

Neural measures also show potential for early clinical prognosis and the implementation of clinical interventions. Neural risk markers for language impairments are particularly relevant as they may allow clinical prognosis *before* behavioral symptoms emerge. Kuhl and colleagues (Kuhl et al., 2013) conducted one of the first studies aimed at identifying potential early neural markers of language outcomes. They used ERPs associated with word processing in 2-year-old children with ASD to predict developmental outcomes at 4 and 6 years. Specifically, the neural signature associated with known words (versus unknown words) was a robust predictor of receptive language scores, cognitive abilities, and adaptive behavior. The predictive utility of this measure increased over time and was particularly robust at predicting scores at 6 years. Neural markers associated with discrimination of native sounds are also predictive of individual differences in language skills at a later age. As noted earlier, Kuhl and colleagues (Kuhl & Rivera-Gaxiola, 2008; Kuhl, 2004) found that the mismatch negativity (MMN) signal measured with EEG-ERP methods can serve as an index of neural speech discrimination in 7.5-month-old infants to predict later rate of language growth. Furthermore, the same neural response measured recently with MEG at 11 months has been used to predict individual differences in expressive syntactic skills (using a spoken grammar task) at 6 years and their risk of developing a speech or language disorder (Zhao, Boorom, Kuhl, & Gordon, 2021).

Identification of early neural markers that predict language skills will ultimately necessitate an understanding of the mechanisms that underlie the relationship between a given marker and language outcomes. Furthermore, large-scale longitudinal studies will be required to ensure that the marker is reliable and reproducible. Research within the first two years of life has the potential to identify neural markers that may predict not only language delays in developmental milestones, but also the emergence of altered neurodevelopmental trajectories. This approach can facilitate the implementation of clinical interventions at the earliest developmental stages when a child's language and social skills are less affected by experiential effects and the brain may be more malleable and responsive to clinical interventions.

5. Methodological considerations: The ecological validity of experimental paradigms

Research on language development has greatly benefited from the use of laboratory-controlled studies in which critical variables are manipulated to isolate specific language abilities or processing mechanisms. In these studies, covariates that would be commonly encountered in the natural world during language learning are removed from the experimental paradigm. This traditional approach, although still fruitful, has received critiques in recent years due to its lack of generalization to real life situations. Researchers across fields of developmental cognitive neuroscience have started to advocate for the use of naturalistic approaches that evoke more ecologically valid patterns of responses than those observed in the laboratory. As noted recently by Cantlon (Cantlon, 2020), a balance can be ultimately achieved between the rigor provided by controlled laboratory methods and the ecological validity of naturalistic conditions. Specifically, the proposal has been to use naturalistic stimuli to i) test the ecological validity of findings observed under controlled conditions and ii) conduct exploratory data-driven analyses that allow discovery of neural patterns and contribute to current theories of brain function. In this section, we add to this debate by considering examples of naturalistic stimuli in infant research and their contribution to our understanding of language development. Furthermore, we discuss how naturalistic stimuli can be combined with neuroimaging techniques to build paradigms that generalize more easily to real-life contexts and that capture fundamental elements of the infant learning experience, such as social cues and their interactive role in the learning process.

Naturalistic conditions utilize any type of stimulus that presents a complex dynamic interaction of multiple elements and therefore requires sustained attention and real-time processing of different types of information (Razi, Seghier, Zhou, Mccolgan, & Zeidman, 2018). The term is relative, and it is frequently used as a contrast with traditional laboratory-controlled stimuli in which several key variables are rigorously selected and controlled for, and environmental factors are removed from the experimental design (Vanderwal et al., 2019). With respect to language comprehension, naturalistic stimuli have been defined as requiring three main criteria: i) the stimulus does not differ from that typically encountered outside of laboratory environments, ii) the stimulus preserves the context in which it would appear in the real word and iii) the subject's motivation to engage with the stimulus in real life is preserved (Hamilton & Huth, 2020). In adults, neuroimaging studies using naturalistic language stimuli often show much more widespread responses (Huth, de Heer, Griffiths, Theunissen, & Gallant, 2016; Lerner, Honey, Silbert, & Hasson, 2011), a less left-lateralized profile of patterns (Cogan et al., 2014; Hamilton, Edwards, & Chang, 2018; Huth et al., 2016) and greater recruitment of higher-order cortical areas (Huth et al., 2016) relative to traditional experimental designs. The three criteria for naturalistic stimuli are particularly relevant in language development since, as noted throughout this article, social factors and how the child interacts with the environment play a critical role in language learning. Therefore, by using ecologically valid paradigms, we can preserve environmental elements that may play a critical role in language learning and reveal otherwise hidden properties of neural responses in natural contexts.

In language developmental research, except for naturalistic diaries or at-home recordings, traditional paradigms for collecting infant data often rely on testing isolated words, sentences, phrases, and occasionally short passages (Ambridge & Rowland, 2013). These paradigms are created based on *a priori* hypotheses about how different levels of linguistic processing are implemented at the neural level. Stimuli are created under precise experimental control, with the goal of rigorously isolating the relevant linguistic elements (Verga & Kotz, 2019). For example, in the statistical learning paradigms reviewed earlier, infants are in a dark room, without an interlocutor and exposed to a series of concatenated sounds that are isolated from any other linguistic or social context. This type of experimental paradigm is theory driven and has led to key discoveries about how language is acquired by infants. A main criticism that these paradigms face, however, is their lack of generalizability. In other words, it is unknown whether the results would be applicable to real-life contexts since critical elements from the environment in which children interact are removed (Aslin & Newport, 2014; Saffran & Kirkham, 2018). For example, in real-world contexts infants are rarely exposed to single words in which there is no interaction with another individual and communication often has a clear social goal. Furthermore, infants' responses in an experiment are influenced by their experience with a specific paradigm, which raises questions regarding the interpretation of results that are collected in tightly controlled laboratory designs (Santolin, Garcia-Castro, Zettersten, Sebastian-Galles, & Saffran, 2021). All these factors make it challenging to understand the extent to which different linguistic and social cues interact and contribute to language learning, unless we implement paradigms that evoke more naturalistic patterns of responses (see Shukla et al., 2011 for an example).

In recent years, a growing number of infant studies have started to use more naturalistic paradigms, following a trend that has emerged in adult language research. These paradigms often require infants to listen to complete stories or watch short video clips, which are drawn from commercial books or movies, thus ensuring they reflect real-world stimuli. These paradigms are engaging and keep the child's attention focused on the presented stimuli. Furthermore, movies are an effective method for reducing motion in children under age 10, which is a main concern in neuroimaging studies (Sanchez-Alonso, Rosenberg, & Aslin, 2021; Vanderwal et al., 2019). Indeed, several neuroimaging studies using naturalistic paradigms have been conducted with infants and older children. For example, EEG responses to brief cartoon movies have been successfully collected in 7-month-olds using multivariate temporal response functions, thus validating the use of this naturalistic paradigm in a pediatric sample (Jessen, Fiedler, Münte, & Obleser, 2019). fMRI has also been used to study language-related brain function in pre-school children (4-to-6-year-olds) using story-listening tasks (Hutton et al., 2017, 2020; Romeo et al., 2018). Neural patterns evoked during naturalistic viewing correlate with developmental behavioral measures such as children's language exposure at home (King et al., 2021; Romeo et al., 2018), mother–child reading behavior (Hutton et al., 2017), episodic memory skills (Cantlon & Li, 2013), social cognitive scores (Richardson, Lisandrelli, Riobueno-Naylor, & Saxe, 2018) and attention abilities (Moraczewski, Chen, & Redcay, 2018). Unfortunately, due to head motion constraints, fMRI data collection with infants and toddlers is challenging, but successful attempts have been made in studies investigating vision (Deen et al., 2017), attention (Ellis et al., 2021) and theory of mind (Richardson et al., 2018; 2020). Furthermore, rigorous approaches to reduce motion artifacts in pediatric fMRI studies have been developed (Grayson & Fair, 2017; Power et al., 2015; Yan et al., 2013). Nevertheless, a common alternative to fMRI movie-watching paradigms in infants and toddlers is the use of resting-state scans during sleep. These scans measure the hemodynamics associated with spontaneous fluctuations of neural activity (Biswal, Zerrin Yetkin, Haughton, & Hyde, 1995; Fox et al., 2005) and can be more easily implemented in younger children (Howell et al., 2019; King et al., 2021). Comparisons of movie-watching and resting-state neural patterns, however, are not straightforward because movie-watching paradigms evoke highly specific patterns of FC that are not present during rest (Perkins et al., 2017; Sanchez-Alonso et al., 2021; Simony et al., 2016). Therefore, cross-age comparisons using movie-watching data with infants and resting-state data with older children or adults are only possible after accounting for state-specific neural patterns (e.g., regressing out movie-watching specific FC). Finally, the use of naturalistic stimuli opens the door to a wide range of analytic approaches. These approaches vary in the extent to which they rely on time-locked signal changes (Vanderwal, Eilbott and Castellanos, 2019) and the existence of an *a priori* specified feature space (e.g., encoding models versus unsupervised dimensionality reduction or inter-subject correlation) (Hamilton & Huth, 2020).

Movie-watching and story-listening paradigms, however, do not include an important component of the language learning experience: the social context. One way to preserve the larger social environment in which daily communications are embedded is to conduct experiments that require an interaction between two individuals. Dyadic interactions can be studied while the child engages in daily activities, such as reading a picture book, playing with toys, or interacting during games (Arunachalam, 2016; Demir-Lira, Applebaum, Goldin-Meadow, & Levine, 2019; Doering, Schluter, & Suchodoletz, 2020; Clemens & Kegel, 2021). In these studies, the infant often interacts with the caregiver or the experimenter, although there are also a few studies that investigate how children process language in interaction with other children (Lytle et al., 2018). These interactive paradigms allow the study of language development in a natural setting in which social cues (e.g., eye gaze, gestures, body movements) and quantity and quality of the interactions (e.g., number of conversational turns, richness of vocabulary, changes in child-directed input) can be characterized with respect to variation in neural measures.

Neural patterns can be collected using simultaneous recording of brain activity from two or more participants using a hyper-scanning paradigm (Montague et al., 2002). A main limitation of hyperscanning studies, however, is that these paradigms do not lend themselves easily to investigate individual differences since each child's experience is interactive and unique. An alternative is to record the child's experience using a head-mounted camera and compare neural responses across children with respect to the same key stimuli, such as reading specific parts of a book or when certain social cues are present. Yet another option is to record video images from the infant's first-person experience using a head-mounted camera and then show these naturalistic scenes to another age-matched infant while simultaneously collecting eye-tracking and neural data (Aslin, 2009). The second infant watches these infant-selected scenarios and responds to the same stimuli without the direct interaction (i.e., under volitional control) with the caregiver or experimenter. This type of design ensures that the two infants are exposed to the same type of stimuli and the results are more likely to be generalizable to naturalistic contexts since the data capture real-time behaviors embedded in the natural environment. A further advantage of this paradigm is that it allows the recording of eye gaze data via an eye-tracker (Aslin, 2009), which provides a more fine-grained assessment of the infant's gaze and it is difficult to do with head-mounted camera videos. This type of hybrid methods are a potentially promising avenue in which to investigate how infants learn in natural environments. In combination with hyperscanning paradigms, they have the potential to reveal how ostensive social signals support synchronized behavior and information transfer during early communication and learning.

6. Concluding remarks

Advances in infant neuroimaging have allowed detailed investigations of the developing brain across a range of non-invasive methodologies. In language neurodevelopmental research, our understanding of developmental trajectories is still limited in comparison to a much more in-depth characterization of behavioral changes and language milestones in the first three years of life. A comprehensive understanding of language neurobiology in early development requires an approach that considers the dynamic nature of the infant brain and the changing computational infrastructure that underlies language learning mechanisms. Accordingly, we have described a framework that includes the essential elements required to build a model of language neurobiology in the infant brain with a focus on auditory language comprehension.

Importantly, developmental change is characterized by substantial differences between-individuals (trait) and within-individuals (state). These differences can be utilized to develop growth curves of both normative and atypical development that enable prediction of language outcomes from neural measurements. Neurodevelopmental periods of maximal state and trait variation at the behavioral level can serve as referent points for biomarker research to investigate differences in neural patterns before the emergence of behavioral manifestations. Collectively, the framework we have described should be useful to connect experimental findings across both neural and behavioral levels with the goal of building robust neurobehavioral trajectories across development that can be predictive of language outcomes.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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