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The Cerebral Bases of Language Acquisition

Ghislaine Dehaene-Lambertz and Claire Kabdebon

INSERM, UMR992, CEA, NeuroSpin Center, University Paris Saclay, Gif-sur-Yvette, France.

Abstract

The development of noninvasive brain-imaging techniques has opened the black box of the infant brain. Instead of postulating theories based on the delayed consequences of, fortunately rare, early lesions, we can now study healthy infant responses to speech. Rather than a brain limited to primary areas or, on the contrary, a poorly specialized brain, brain-imaging studies have revealed a functional architecture in infants that is close to what is described in adults. In particular, a hierarchy of increasingly integrated computations is observed along the superior temporal regions, and the processing of different speech features is already segregated along parallel neural pathways with different hemispheric biases. Yet, although highly structured, the infant brain still differs from the adult brain, with particularly delayed brain responses arising from frontal regions. We can expect that a better understanding of the computational abilities of this early network may provide insight into the mechanisms underlying language acquisition.

Speech is a remarkable communication device whose efficiency to convey information is based on the combination of units (phonemes in words, words in sentences) according to rules. Before the end of the first year of life, human infants display amazing capacities in processing speech. First, they show an extraordinary ability to analyze the auditory content of the speech stream. They learn the repertoire of sounds (or phonemes) used by their native language (Kuhl, Williams, Lacerda, Stevens, & Lindblom, 1992; Werker & Tees, 1984) and the rules (phonotactics) for combining these sounds within words (Jusczyk, Luce, & Charles-Luce, 1994). They notice the frequent words of stories they have heard a few times (Jusczyk & Hohne, 1997) and that content words are surrounded by recurrent syllables (e.g., ing, the, a) that have a different function in the sentence (Shi, 2014), as they start to figure out sentence organization. This early learning is based on distributional analyses at different levels of the linguistic structure, from the syllabic level (Saffran, Aslin, & Newport, 1996) to a more abstract level, such as word category (Gervain, Nespore, Mazuka, Horie, & Mehler, 2008). Second, they rapidly discover the referential aspect of speech: they know that speech conveys information from at least 4 months of age (Marno et al., 2015), and at 6–9 months of age, they already know the meaning of a few words, such as mommy, hug, some body parts, and more (Bergelson & Swingley, 2012; Tincoff & Jusczyk, 1999). Third, infants might also rapidly understand that speech is a symbolic system. They can create equivalence between a label and a category (Kabdebon & Dehaene-Lambertz, 2019), which helps them to sort items into named categories (e.g., dinosaur vs. fish pictures; Ferry, Hespos, & Waxman, 2013).

What are the cerebral bases of these impressive competences? Is language acquisition based on a functional organization similar to the adult linguistic network? This question is not trivial, as the development of the human brain is complex and extends over two decades. Its weight increases from 400 g at birth to 1400 g in adults. The organization of cortical layers and large fiber networks is well established at term birth (Dubois & Dehaene-Lambertz, 2015), although neuronal migration is still ongoing in the frontal areas during the first months of life (Paredes et al., 2016). Maturation consists of waves of synaptogenesis followed by pruning with an acceleration of signal transmission speed due to myelination of the tracts. These phenomena are relatively well described, but brain maturation covers many other aspects essential to the effectiveness of neural networks, such as the maturation of glia and various types of neurons, the production of neurotransmitters, changes in receptors, the accumulation of proteoglycan chains, and more, whose maturational sequences are unknown in the human brain. Additionally,

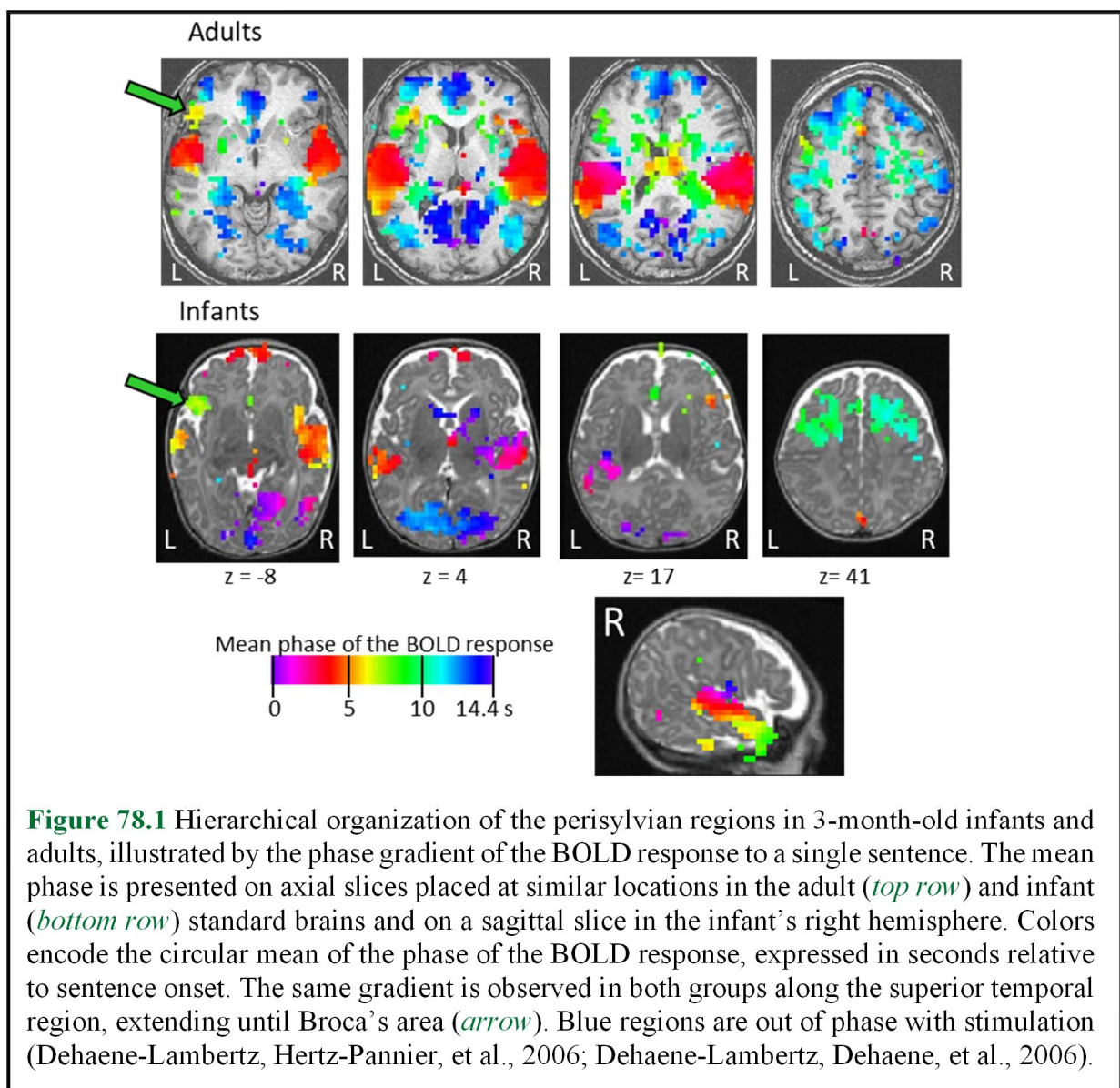
depending on the region, maturational spurts occur at different moments and at different rates, generating dynamic shifts within and between regions and adding a dimension of complexity to how networks interact. Although the description of the immature human brain becomes more refined thanks to the development of noninvasive brain-imaging techniques, we are still far from understanding what crucial features of the infant brain allow for this rapid linguistic development. Nevertheless, based on the brain-imaging data acquired from the last trimester of gestation onward, we can start to propose hypotheses on how the functional architecture of the infant brain may explain some of the early linguistic competencies.

The Organization of Perisylvian Regions

In human adults, linguistic and nonlinguistic representations of speech are computed in parallel along distinct hierarchical pathways in the superior temporal lobe, reaching the inferior frontal regions. This hierarchical and parallel functional organization is already observed in infants' perisylvian regions.

A hierarchy of linguistic processes When infants—even neonates—listen to speech, activation occurs along the superior temporal region bilaterally and extends to distant left inferior parietal and frontal regions (Dehaene-Lambertz, Hertz-Pannier, et al., 2006; Pena et al., 2003; Shultz, Vouloumanos, Bennett, & Pelphrey, 2014; Sato et al., 2012). Interestingly, the phase of the BOLD response progressively slows down as we move away from the primary auditory cortex (Heschl's gyrus) toward the temporal pole and toward the temporoparietal junction (Dehaene-Lambertz, Hertz-Pannier, et al., 2006). Whereas the Blood Oxygen Level Dependent (BOLD) response rapidly peaks and decreases in Heschl's gyrus, it becomes more and more delayed and sustained anteriorly in the superior temporal sulcus and even starts at the end of a sentence in the most anterior regions (figure 78.1). This temporal gradient is not related to an immature neurovascular coupling since a similar, although faster, gradient is visible in adults (Dehaene-Lambertz, Dehaene, et al., 2006). Because in infants, as in adults, the superior region of the temporal areas is more sensitive to acoustic features than the more ventral regions involved in the computation of abstract and integrated representations (Bristow et al., 2009; DeWitt & Rauschecker, 2012), we proposed that this gradient might be the consequence of the hierarchical organization of the perisylvian networks: the increasingly delayed and sustained responses would correspond to larger and larger windows for integrating speech chunks, as described in adults (Ding, Melloni, Zhang, Tian, & Poeppel, 2016).

Such hierarchical organization might explain infants' early sensitivity to sentence organization and why they prefer listening to sentences with pauses located at prosodic boundaries rather than within prosodic units (Hirsh-Pasek et al., 1987). With its embedded units, the prosodic hierarchy is a natural input for these regions, helping infants segment the speech stream into coherent chunks. Analyses can then be restricted to each prosodic unit, explaining why the computations of transitional probabilities between syllables—which is the main proposed mechanism in infants for extracting words from a stream of speech (Saffran, Aslin, & Newport, 1996)—cannot occur across a prosodic boundary (Shukla, White, & Aslin, 2011). Finally, as prosody and syntax are tightly related, this hierarchical organization might also secondarily facilitate the learning of native syntax (Christophe, Millotte, Bernal, & Lidz, 2008).



Parallel pathways for voice and phoneme processing Speech conveys information not only about the language but also about the speaker. Both elements are crucial for infants to understand what is said and to identify who is speaking. Thus, they should simultaneously neglect local variations in timbre, pitch, speech rate, and so on to extract the linguistic information and use them to be able to keep track of the speaker's identity, actual emotion, and location in space. Using event-related potentials (ERPs), we showed that these computations are done in parallel: After a series of repeated auditory-visual vowels, a change in vowel identity or the speaker's gender evokes two different mismatch responses, characterized by a different voltage topography on the scalp but within the same time window, in 3-month-olds (Bristow et al., 2009). Although spatial information is coarse with electroencephalography (EEG), a model of brain sources suggests a right-lateralized response for the change of voice, contrasting with a left-lateralized response for a change of vowel.

These hemispheric biases are confirmed with functional magnetic resonance imaging (fMRI) in 2-month-old infants who listened to their mother's voice or to the voice of an unknown mother. In the left posterior temporal region, activations are enhanced in response to the voice of one's own mother, probably because familiarity with the voice allows for better phonetic access. Right-hemisphere differences are also observed in a more anterior temporal region, described as the voice region in adults. This region is also found when nonlinguistic vocal sounds are contrasted with environmental sounds in 3- to 7-month-olds (Blasi et al., 2011). All of these experiments underline a parallel organization from the first months of life channeling voice and phoneme processing along different pathways.

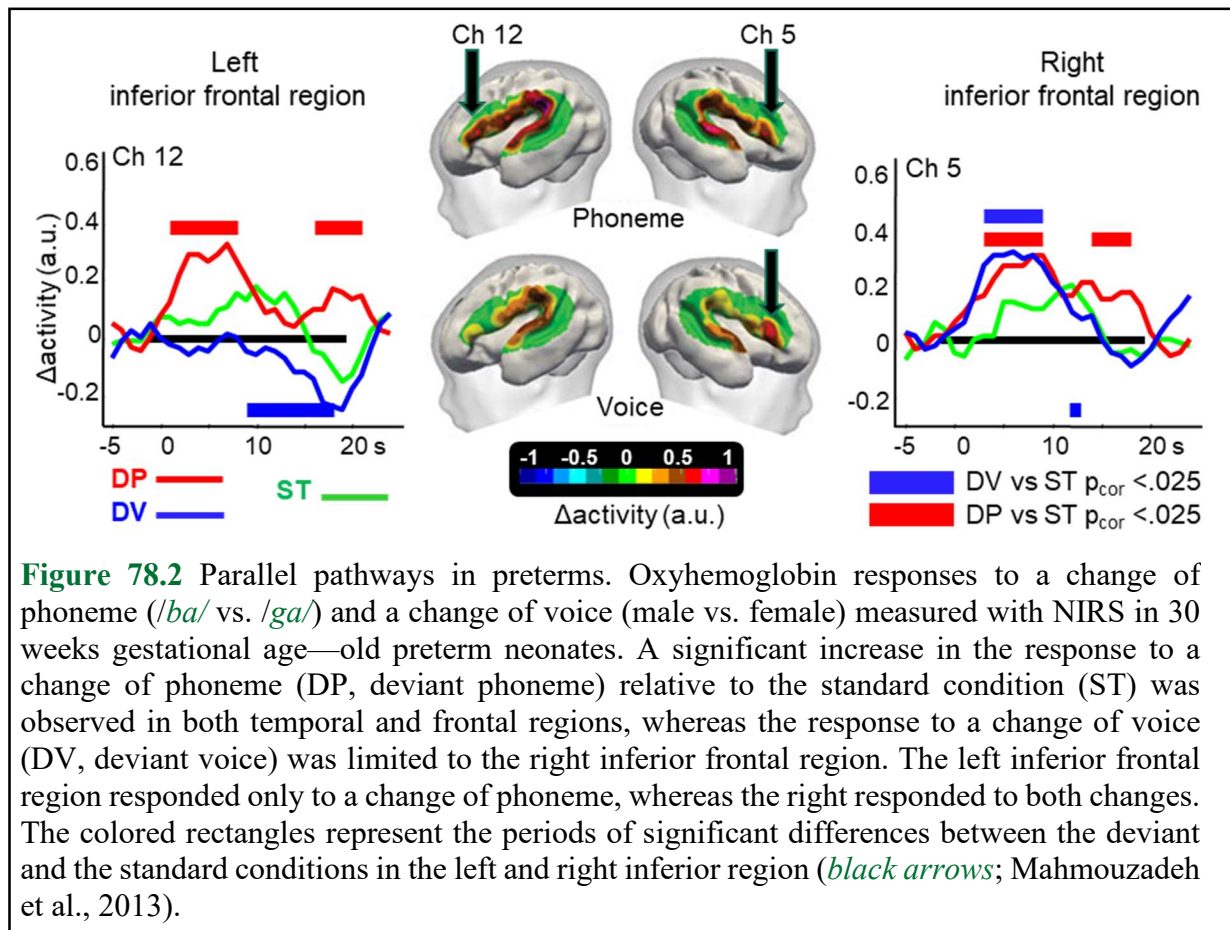
Early lateralization of speech processing The previous studies suggest that adults' left-right functional differences have their roots in early development. Indeed, a larger left-hemispheric response is reported in most studies using speech during the first trimester of life: at the level of the *planum temporale* in fMRI studies (Dehaene-Lambertz, Dehaene, & Hertz-Pannier, 2002; Dehaene-Lambertz, Hertz-Pannier, et al., 2006; Dehaene-Lambertz et al., 2010) and less precisely over the superior temporal region in near-infrared spectroscopy (NIRS) studies (Pena et al., 2003; Sato et al., 2012; Vannasing et al., 2016). Activations in response to one's native language are also more left-lateralized than to music (Dehaene-Lambertz et al., 2010) and to other biological sounds, such as nonspeech vocalization, footsteps, and monkey calls (Shultz et al., 2014), but not compared to a foreign language and backward speech (Dehaene-Lambertz, Dehaene, & Hertz-Pannier, 2002), at least initially. After a few months,

however, the difference between native and nonnative speech becomes larger. Five-month-olds, but not 3-month-olds, show larger NIRS activation for their own dialect than for a foreign dialect (Quebecois vs. Parisian French) over only the left, but not the right, temporal region (Cristia et al., 2014). A left-hemispheric advantage to process fast temporal transitions (Zatorre, Belin, & Penhune, 2002) might explain an early left bias for speech-like stimuli that is further reinforced through linguistic experience. However, the fact that sign language is also left lateralized in adults argues for a multifactorial contribution to the robust left lateralization of language in humans (see chapter 73).

A Precise Temporal Encoding since the Fetal Life

This functional organization finds its roots during fetal life. At 6 months gestation, 3 months before term, the subcortical sensory system begins to react to external sounds, and the thalamocortical connections reach the cortical plate, feeding the first cortical circuits with external information (Kostovic & Judas, 2010). Although the local microcircuitry is very different from later ages since most of the neurons are still migrating to reach their final location and dendritic trees are sparse, the brain's general connectivity is already visible at the structural (Takahashi, Folkerth, Galaburda, & Grant, 2011) and functional level (Fransson et al., 2007; Smyser, Snyder, & Neil, 2011). Already at this age, preterm neonates react to a change of consonant (/ba/ vs. /ga/) and to a change of voice (male vs. female) randomly occurring in a series of repeated syllables (figure 78.2). Furthermore, as in older infants, the temporal and spatial responses generated by both types of changes measured with EEG and NIRS are different, with larger and more mature responses for the change of phoneme than for the change of voice, revealing not only that these two features are processed differently but that the human brain is very sensitive to the temporal dimension of speech from the onset of the thalamocortical circuitry (Mahmoudzadeh et al., 2013; Mahmoudzadeh, Wallois, Kongolo, Goudjil, & Dehaene-Lambertz, 2017).

These results are not trivial since anesthetized rats tested in the same paradigm reacted more strongly to a change in voice than consonant, with a right-lateralized response for both changes (Mahmoudzadeh, Dehaene-Lambertz, & Wallois, 2017). Rats also display a strong reaction to differences in voice, obscuring language discrimination (Toro, Trobalon, & Sebastian-Galles, 2005). By contrast, human adults and infants are commonly better at recovering linguistic content, even for different voices, than at recognizing the same voice for different linguistic content (Dehaene-Lambertz, Dehaene, et al., 2006; Johnson, Westrek,



Nazzi, & Cutler, 2011), suggesting a particular human sensitivity to linguistic features beyond general mammal auditory responses. A fine temporal encoding of the auditory world, observed from 30 weeks of gestational age onward, might be one of the important human auditory features.

Several experiments have illustrated the relation between the precision of temporal encoding and better performance in tasks using speech stimuli in normal subjects. For example, Kabdebon et al. (2015) recorded high-density EEG in 8-month-old infants while they were listening to a stream of syllables concatenated according to an AxC structure (i.e., the first syllable (A) predicted the third syllable (C) of successive triplets whereas the middle syllable (x) is variable). The infants were then tested with isolated trisyllabic words that either respected or did not respect the hidden structure of the training stream. The difference between these two conditions at test was significantly correlated with the temporal locking to the syllable frequency during the training stream, as observed with EEG. Similarly in adults, the temporal similarity between auditory cortical activity and speech envelopes predicted speech comprehension (Ahissar et al., 2001). A deficit in temporal encoding has been proposed as one of the mechanisms underlying some oral and written language impairments (Abrams, Nicol,

Zecker, & Kraus, 2009; Lehongre, Ramus, Villiermet, Schwartz, & Giraud, 2011), and the size of the production lexicon can be predicted from the performance of a phonetic discrimination task at 6 months (Tsao, Liu, & Kuhl, 2004). Lexicon size is also correlated with the speed of recognition of auditorily presented words at 18 months (Fernald, Perfors, & Marchman, 2006), demonstrating the interplay between early refined phonetic encoding abilities and later higher-level linguistic abilities.

Immature but Nonetheless Functional Frontal Areas

Activation to speech does not remain limited to auditory areas but extends to higher levels in the parietal and frontal lobes (figures 78.1 and 78.2). Because of their protracted development, frontal areas were classically assumed to function poorly in infants. Many brain-imaging studies have now revealed their involvement in infant cognition: the inferior frontal region reacts to a change in auditory sequences as early as 6 months gestation, on the left for a change of phoneme and on the right for both a change of voice and a change of phoneme (Mahmoudzadeh et al., 2013). At 3 months post-term, an increase in activation in the frontal areas is observed in response to the repetition of a short sentence (Dehaene-Lambertz, Hertz-Pannier, et al., 2006) or in response to repetition of the same vowel across modalities (Bristow et al., 2009). Enhanced frontal activations are also recorded when a complex auditory pattern is violated (Basirat, Dehaene, & Dehaene-Lambertz, 2014). These results reveal the frontal regions' involvement in short-term memory. At the same age, recognition of the prosodic contours of one's native language activates the right dorsolateral prefrontal region in attentive infants (Dehaene-Lambertz, Dehaene, & Hertz-Pannier, 2002), whereas voice familiarity modulates the balance between the median prefrontal regions, sensitive to stimulus familiarity, and the orbitofrontal limbic circuit, involved in stimulus emotional valence (Dehaene-Lambertz et al., 2010). Thus, the frontal lobes in infants are not only activated but are also parceled into different regions distinctively engaged depending on the task, exactly as in older participants.

However, frontal regions react at a slower pace in infancy than later in life. ERP studies have shown that late responses, which depend on higher levels of processing, are disproportionately slower in infants, relative to adults, compared to the infant-adult differences in early sensory regions. Electrical components proposed to be the equivalent of the adult P300 have been recorded after 700 ms, and even around 1 s, until at least the end of the first year (Kouider et al., 2013). By contrast, the latency of the visual P1 reaches adult values around 3

months of age (McCulloch, Orbach, & Skarf, 1999). These time delays should be further studied to analyze whether, and how, they might confer an advantage in learning.

Because maturation improves both local computations and the speed in the connections between regions, the balance between networks may change with development, and patterns of maturation may thus reveal the crucial role of certain circuits at a given moment in acquiring new skills. Adjusting the weights of the different pathways—and thus how they learn—through maturational lags at precise nodes of the perisylvian cortex might be a way to genetically control language development. Combining different techniques makes it possible to study this question—for example, the efficiency of the dorsal and ventral pathway connecting inferior frontal areas and superior temporal areas. A longitudinal study of the functional connectivity over the first 2 years of life reports a rapid increase of connectivity within the left linguistic network between the frontal and posterior temporal areas within the first year of life (Emerson, Gao, & Lin, 2016). At the structural level, the T2 MRI signal component, which is sensitive to free water in the tissues, and diffusion tensor imaging (DTI), which provides measures of the movement of water molecules (measures of diffusivity) and their direction (measure of fractional anisotropy), can be used to study gray and white matter maturation. These markers show that structures belonging to the dorsal pathway (frontal area 44, the posterior superior temporal sulcus, and the arcuate fasciculus) mature in synchrony. While the dorsal pathway displays a delayed maturation relative to the ventral pathway, it starts to catch up after 3 months of age (Dubois et al., 2015; Leroy et al., 2011). This adjustment might be related to the increase in vocalization and progression in the analysis of the segmental part of speech observed at the same age.

The involvement of the inferior frontal regions and the dorsal pathway provides infants with a short-term auditory memory, which seems to be lacking in macaques (Fritz, Mishkin, & Saunders, 2005). A long buffer may favor the discovery of second-order rules by keeping track of segmental elements (Basirat, Dehaene, & Dehaene-Lambertz, 2014; Kovacs & Endress, 2014). Coupled with hierarchical coding along the superior temporal regions, this may favor computations on chunks of chunks and increase sensitivity to deeper hierarchical structures, as well as algebraic rules, as demonstrated in 8-month-olds (Marcus, Vijayan, Bandi Rao, & Vishton, 1999). The early role of the dorsal pathway is confirmed by the observation that fractional anisotropy values measured at term birth in the arcuate fasciculi are correlated with linguistic scores at 2 years of age (Salvan et al., 2017).

When infants listen to speech, activations are not limited to the classical linguistic areas, and the involvement of frontal areas outside the linguistic system may improve infants' focus on speech as a relevant stimulus. Motivation and pleasure, as well as understanding the referential aspect of speech through social cues, have been shown to be important for speech learning (Kuhl, Tsao, & Liu, 2003). The activation in dorsolateral prefrontal regions shown in awake infants recognizing their native language, as well as activation in prefrontal median regions when the voice is familiar, may very well explain these behavioral observations.

Nature versus Nurture

During the first year of life, infants become attuned to the prosody and phonetic repertoire of their native language (Kuhl, Williams, Lacerda, Stevens, & Lindblom, 1992; Werker & Tees, 1984), which can have long-term effects. Chinese adoptees in Quebec, no longer exposed to Chinese after the first year of life, on average, still perceive a tonal contrast and activate the left planum temporale similarly to native Chinese speakers. This contrasts with French-speaking controls never exposed to Chinese, who activate only the right hemisphere (Pierce, Klein, Chen, Delcenserie, & Genesee, 2014). Because preterm infants are exposed earlier than full-term neonates to aerial speech, they can be compared to full-term neonates to study the effects of *ex-utero* exposure versus the brain's developmental age on the sensitivity to foreign speech. In two different studies in preterm infants, Pena and colleagues reported that the decrease in the sensitivity to foreign-language prosody (Pena, Pittaluga, & Mehler, 2010) and foreign phonetic contrasts (Pena, Werker, & Dehaene-Lambertz, 2012) is related to the brain's developmental age rather than the duration of *ex-utero* life. By contrast, learning the phonotactic rules of one's native language is dependent on the duration of exposure to aerial speech (Gonzalez-Gomez & Nazzi, 2012). This discrepancy may point to a critical distinction between a learning mechanism (here, statistical learning allowing for the accumulation of positive evidence on the frequency of phonetic categories and combinations of phonemes) and the critical period during which this learning mechanism is workable. In the mouse visual cortex, it has been proposed that the opening and closing of "critical" windows relies on two thresholds in the accumulation of a homeoprotein, Otx2, in GABAergic parvalbumin interneurons (Hensch, 2004). When the Otx2 level reaches one threshold, learning starts; when it reaches the other, learning then stops or at least becomes more difficult. A similar mechanism might explain how computation of the statistics of the native phonetic environment can only begin after a certain maturational age (probably after 35 weeks gestational age, when the

migration and maturation of interneurons is sufficiently advanced, but no study has yet examined this point) and stops around the end of the first year, when the second threshold is reached.

Conclusion

We have emphasized here the early brain organization and its similarities with adult networks and have sought to relate brain-imaging results to behavioral performance. This architecture and its complex maturational calendar have been selected through human evolution as the most efficient in helping infants detect correct cues in the environment in order to learn their native language. A better understanding of brain plasticity and, notably, its changes with age and learning at the microstructural and network levels is a necessary step to refine models of language acquisition.

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