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Neurodevelopmental Preparedness for Language in the Neonatal Brain

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Abstract

Neonates show broad-based, universal speech perception abilities, allowing them to acquire any language. Moreover, an increasing body of research shows that prenatal experience with speech, which is a low-pass signal mainly preserving prosody, already shapes those abilities. In this review, we first provide a summary of the empirical evidence available today on newborns' universal and experience-modulated speech perception abilities. We then interpret these findings in a new framework, focusing on the role of the prenatal prosodic experience in speech perception development. We argue that the chronological sequence of infants' experience with speech, starting before birth with a low-pass filtered signal and continuing with the full-band signal after birth, sets up the prosodic hierarchy and a cascade of embedded neural oscillations as its brain correlate, laying the foundations for language acquisition. Prosody, constituting infants' very first experience with language, may thus play a fundamental role in speech perception and language development.

Key words:

speech perception, newborn infants, prenatal experience, prosody, language acquisition, neural oscillations

1. Introduction

Legend has it that the Holy Roman Emperor Frederick II (1194-1250 AD) ordered newborn infants to be clad, fed and appropriately cared for appropriately in every possible way, but never to be talked to. This experiment, if it ever was conducted, was one of the first attempts to understand what inborn, biologically endowed propensities human infants bring to the task of acquiring language and what knowledge comes from later experience. This question is far from being settled and has continued to puzzle scholars and the general public ever since. Fortunately, since the last decades of the twentieth century, we no longer need to use such ethically dubious methods to shed light on the issue, as non-invasive methods became available to test even the youngest infants' language abilities. This review motivates the theoretical relevance of investigating newborns' speech perception and language learning abilities, and summarizes the most important empirical findings from this research area. We then interpret this body of evidence using a novel model of language development that highlights the importance of prenatal experience in shaping early speech perception and language abilities.

1.1 Why study newborns?

After the dominance of behaviorism, the 1950's-1960's brought about what was later termed the "cognitive revolution" – a new perspective on human psychology that emphasized internal mental representations and abilities even if they were not readily observable in overt behavior. Noam Chomsky's work on language was one of the foundations of this cognitive movement. Chomsky (1959) argued that humans have a productive use of language, being able to express contents never heard or produced before, of theoretically infinite length (e.g. "Jim said that

Ray believed that Robbie argued that John thought that...."). This can be achieved only if children do not learn language by copying and imitating what is said in their environment, but rather possess a mental ability (i.e. a grammar) to generate language. Chomsky assumed that the ability to learn language was thus innate, and that the young learner's task when acquiring a specific language (e.g. Chinese, French or Zulu) was to configure this innate ability on the basis of the restricted input they hear. Chomsky drew a parallel between the languagelearning child and the linguist who works on an unfamiliar language. They both need to establish the grammar and vocabulary of the target language on the basis of the linguistic data they observe. From a mathematical perspective, this task is unsolvable, since the learner runs into the induction problem: For any finite dataset, there is an infinite number of underlying rule systems that could have generated them. It is, therefore, impossible to learn language on the basis of the input alone. If the child does not have innate guiding principles for choosing between the infinitely many possible rule systems, he/she will not be able to acquire any, and even if he or she chooses one rule system, there will be no guarantee that this will converge with those acquired by other infants. Yet, learners exposed to the same language in a given community develop functionally similar grammars. Chomsky concludes that given the finite nature of the input dataset and the remarkable speed and ease with which human infants learn language, assuming an innate language faculty is a logical necessity.

This position was later countered by opposing empirical theories (e.g. Elman et al. 1997; McCauley & Christiansen 2019; Tomasello 2000) that claimed that the input may be much richer than Chomsky argued, complete with not only with large quantities of language input, but also with convergent non-linguistic cues, such as physical objects and most importantly social partners. As a consequence, they argued, language may be acquired through non-specific learning and cognitive abilities such as analogies, statistical learning,

theory of mind and joint attention etc., without a need for assuming an innate languagespecific ability.

As a consequence of this controversy (the "nature-nurture" debate), empirical research into young infants' speech perception, language learning and other cognitive abilities, has gained high theoretical relevance. Evidence for the early presence of an ability was often interpreted as evidence for its innate nature, whereas its absence early in development was taken to mean the ability is learned. Mapping the "initial state" of language development, before experience begins, has become particularly important. This has increased interest in investigating newborn infants' speech perception abilities, since newborns are the youngest population that can easily be tested in experimental studies [although methods exist to test fetuses, these options are more limited for obvious practical reasons; Dubois et al. 2014; Huotilainen et al. 2005; Weikum et al. 2012)].

Concurrently, attention has also focused on what experience babies might have with language prenatally. Hearing is functional from about the twenty-fourth to the twenty-eighth week of gestation, depending on the specific auditory function measured (Eggermont & Moore 2012). Newborns thus already have experience with language before birth and do not represent the true "initial state". Describing this experience is, therefore, important for interpreting the abilities observed in newborns. While directly observing the fetal auditory environment is challenging in humans, research with animal models, computational simulations and fetal measures (e.g. Abrams & Gerhardt 2000; DeCasper & Sigafoos 1983; DeCasper et al. 1994; Gerhardt et al. 1992; Granier-Deferre et al. 2011; Griffiths et al. 1994; Jardri et al. 2008; Querleu et al. 1988) suggests that maternal tissues and fluids act as low-pass filters. Fetuses thus receive a speech signal that is quite different from their post-natal

speech experience, and consists mainly of prosodic information. How this prenatal experience impacts newborns' speech perception abilities is starting to be better understood.

With the advent of brain imaging techniques and advances in genetics and epigenetics, it has become increasingly clear that the strict dichotomy of nature or nurture cannot offer an appropriate framework for explaining language development. A more synergistic view has emerged emphasizing how genetically endowed and experience-dependent processes interact to bring about development (Choi et al. 2018; Gervain & Mehler 2010; Werker & Tees 2006). Under this view, the main focus is no longer to ask whether innate or learned mechanisms are responsible for language development, but rather to investigate how such mechanisms converge and interact. When discussing the newborn brain's readiness for language, we take this interactive view, highlighting both those universal abilities that newborns bring to the task of acquiring language (Section 2), and those already shaped by speech heard in the womb (Section 3). We will then propose a new model for very early language development based on the chronology of infants' experience with speech (Section 4).

1.2 How to study newborns?

Before summarizing the empirical results, we briefly introduce some of the main methods used to assess newborns' speech perception and language learning abilities. Newborns, like young infants in general, are challenging research participants, with a limited attention span, a restricted behavioral repertoire, and an inability to follow instructions or to provide verbal answers. It is nevertheless possible to conduct behavioral experiments relying on newborns' spontaneous behaviors and brain imaging techniques now allow us to probe the newborn brain non-invasively.

The most commonly used behavioral measures for the assessment of various perceptual and cognitive abilities in newborns include heart rate, a technique also used with fetuses (Della Longa et al. 2021; Nagy & Molnar 2004), looking times (Izard et al. 2009; Johnson et al. 1991), and high-amplitude (or non-nutritive) sucking (HAS) (Floccia et al. 1997). HAS, the method most frequently used to study speech perception in newborns, relies on a spontaneous increase and intensification of newborns' sucking behavior when exposed to sound stimuli that are of interest to them. This response can be measured with a pressure transducer built into a pacifier that the infants suck on. This technique is most often used to measure newborns' spontaneous preference between two types of stimuli or their ability to discriminate between them (Byers-Heinlein et al. 2010). To measure preference, infants are typically presented with two types of stimuli (e.g. two languages) in different blocks (e.g. of 1 minute each). A greater number of high-amplitude sucks across blocks for one stimulus type indicates preference. Discrimination, by contrast, is often measured using a habituation / dishabituation design, whereby neonates are first habituated to one type of stimulus (e.g. one language). Once their sucking rate falls below a predefined habituation criterion, a new stimulus type (e.g. another language) is presented. If newborns increase their sucking rate after the switch, this indicates that they have noticed and responded to the change and can thus discriminate the two stimuli. Another group, the control, is tested with a switch involving a change in stimulus tokens (e.g. change in speaker), but not in stimulus type/category (e.g. no change in language). In this group, sucking rate is expected to continue decreasing after the switch, showing that the dishabituation in the experimental group is not due to low level properties of the stimulus change.

More recently, brain imaging techniques have also been applied to investigate the newborn brain and map the neural basis of different cognitive processes. The two most commonly used techniques, both non-invasive and well-tolerated by infants, are

electroencephalography (EEG) (De Haan 2013) and its less frequently used magnetic equivalent, magnetoencephalography (MEG) and near-infrared spectroscopy (NIRS) (Gervain et al. 2011; Lloyd-Fox et al. 2009). EEG measures electrical brain activity (generated by pyramidal cells) recorded from electrodes placed on the scalp. The EEG technique has high temporal resolution (in the millisecond range) but does not provide good spatial localization due to the inverse problem, i.e. that electrical potentials travel in all directions and the signals picked up at different electrodes are a mix of the potentials originating from different sources in the brain. (Mathematical techniques to solve the inverse problem and allow source localization exist, but are less often used with infant data, as modeling the infant head and brain anatomy is not as advanced as adult head modeling (although see Lew et al. 2013; Roche-Labarbe et al. 2008.) EEG (and MEG) data may be analyzed as (a) event-related potentials, that is, electrical changes in brain activity time-locked to a stimulus, or (b) neural oscillations, that is, neural activity in a specific frequency band (i.e. delta 1-3Hz, theta 4-8Hz, alpha 8-12Hz, beta 12-30Hz, gamma > 30Hz). NIRS uses red and near-infrared light of low intensity to illuminate the surface (~0.5-1.5cm) of the cortex and thereby measure the attenuation of light caused by concentration changes in oxygenated and deoxygenated hemoglobin, which are hemodynamic indicators of local neural activity. As a result, NIRS does not measure neural activity directly, only its hemodynamic correlates. The hemodynamic response is slow and as a result, NIRS has low temporal resolution (in the second range), but offers precise spatial localization, as it is not subject to the inverse problem [even if the resolution is low compared with magnetic resonance imaging (MRI)]. NIRS and EEG can also be combined (Cabrera & Gervain 2020; Telkemeyer et al. 2009; Wallois et al. 2012), as the two signals do not interfere with each other and the two types of sensors can be placed into the same headgear, typically a stretch cap. NIRS-EEG co-recording has the advantage of offering both high spatial and temporal resolution.

2. Universal Speech Perception Abilities

Newborn infants have remarkable speech perception abilities. With an auditory system that is functional, but not yet fully mature (Eggermont & Moore 2012), they can flexibly start acquiring any language(s) they are exposed to. Indeed, humans are born "linguistic citizens of the world". This ability is rooted in broad-based perceptual sensitivities allowing newborns to discriminate most linguistic contrasts that appear in the world's languages.

The first task newborns face is to identify speech among the various sounds in their environment. Newborns and 2-month-old infants can indeed recognize speech, and show a strong preference for it over equally complex sine wave analogues (Vouloumanos & Werker 2004). However, the category "speech" may be relatively broad at birth roughly corresponding to primate vocalizations, as newborns show equal preference for human speech and rhesus monkey vocalizations when tested on short words vs. vocalizations (Vouloumanos et al. 2010). It is only by 3 months that infants show a unique preference for speech over both sine wave analogues and monkey calls (Vouloumanos et al., 2010). It may be the case, though, that longer speech utterances with a full intonational contour may elicit a preference over monkey calls already at birth, if prenatal experience with prosody impacts newborns' perceptual preferences, as discussed in Section 1.1.

Not only do newborns identify language in their environment, but they can also discriminate languages from one another, even if those languages are unfamiliar to them, on the basis of their different rhythms (Mehler et al. 1988; Nazzi et al. 1998; Ramus et al. 2000). Language rhythm is quantified along different acoustic dimensions, such as %V, i.e. the relative proportion of vowels in the speech signal as well as Δ C and Δ V, the variability in the length of consonant and vowel clusters, respectively (Ramus et al. 1999). On the basis of

these metrics, languages can be grouped into three classes: Mora-timed languages like Japanese, syllable-timed languages like French or Italian and stress-timed languages like English and Polish. For instance, mora-timed and syllable-timed languages have relatively high %V and simple syllable structure with little variation in ΔC , while stress-timed languages like English and Polish have lower %V with more complex syllables, reflected in higher ΔC . [Other metrics also exist to quantify rhythm; Dellwo 2006; Grabe & Low 2002; Loukina et al. 2011; Wiget et al. 2010).]

Importantly, rhythmic discrimination does not require familiarity with the languages: Newborns prenatally exposed to French are able to discriminate between English and Japanese. Tamarin monkeys can as well (Ramus et al. 2000), suggesting that rhythmic discrimination might be a general property of the primate or mammalian auditory system. One important implication of newborns' ability to discriminate languages on the basis of rhythm is that infants born into a multilingual environment can immediately detect that they are being exposed to different languages, at least if those languages are rhythmically different. Bilingual newborns have indeed been shown to be able to discriminate their two languages from a third, rhythmically different language (Byers-Heinlein et al. 2010).

Newborns are thus equipped to identify speech in their environment, even in different languages. What linguistic units do they use to represent speech? They readily detect the acoustic cues correlated with word boundaries (Christophe et al. 1994). They have also been found to be sensitive to the prosodic makeup of words at the syllable level (Sansavini et al. 1997), readily discriminating words with different lexical stress patterns, that is, stress-initial (trochaic) vs. stress-final (iambic). Interestingly, however, they cannot tell apart words with different numbers of phonemes, if the number of syllables is the same in the two words (Bijeljac-Babic et al. 1993). They are also sensitive to the universal phonotactic constraints governing syllable structure and the distribution of consonants within syllables, known as the

sonority hierarchy (Gómez et al. 2014). These results have been interpreted to suggest that the syllable is a privileged unit of representation for speech in young infants (Mehler et al. 1996). Recent EEG results (Cabrera & Gervain 2020; Ortiz Barajas et al. 2021) suggest that newborns, like adults, are indeed able to track the speech envelope (i.e. the amplitude modulation) of the speech signal, which roughly corresponds to the syllables / syllabic rate.

Young infants can also discriminate many of the phonemes appearing in the world's languages, as has been shown both behaviorally (Eimas et al. 1971 and subsequent work) and electrophysiologically (Dehaene-Lambertz & Baillet 1998). This universal discrimination repertoire is one of the hallmarks of young infants' broad-based abilities, allowing infants to learn any language they are exposed to. As with the case of rhythm, animals can also discriminate phonemes categorically, at similar acoustic boundaries as humans do (Kuhl 1981, 1986), suggesting that phoneme perception is a basic ability rooted in general mammalian auditory mechanisms.

It needs to be noted, however, that most evidence is from infants two-to-three months of age and older. Newborns' phoneme representations have rarely been tested (Cheour et al. 2002, Dehaene-Lambertz & Pena 2001). One existing study suggests mature discrimination abilities at least for native stop contrasts that are robust enough to be maintained, like in adults, even for impoverished speech signals vocoded to preserve only the lowest (<8Hz) amplitude modulation cue (Cabrera & Gervain 2020).

Some studies, especially from non-Indo-European languages, suggest that some particularly challenging contrasts may emerge later (e.g. through refinement of existing categories) and may not be part of the initial repertoire (Mazuka et al. 2014, Narayan et al. 2010). The open questions about the initial repertoire notwithstanding, phoneme perception undergoes important perceptual reorganization on the basis of language experience during the first year of life, with infants maintaining or even gradually improving their ability to

discriminate contrasts found in their native language, but in many cases losing the ability to discriminate non-native ones (e.g. Werker & Tees 1984). The discussion of this exciting developmental process is beyond the scope of the current review, but many excellent summaries exist (Gervain & Mehler 2010, Kuhl 2004, Swingley 2021, Werker 2018, Werker & Curtin 2005).

Newborns not only are sensitive to the sound patterns of language, but also show abilities that allow them to begin learning about language structure. They can discriminate the two universal lexical categories of functors, that is, words that mark morphosyntactic structure (e.g. the, she, in, up etc.), and content words, words that carry lexical meaning (e.g. door, rainbow, run, beautiful etc.), on the basis of the different phonological properties of the two categories (Shi et al. 1999). Newborns are also sensitive to word order, and can detect the violation of the serial order in sequences of words (Benavides-Varela & Gervain 2017). They can also detect more abstract patterns, such as repetition-based regularities like ABB (e.g. "mu ba ba", "pe na na" etc.) or AAB (e.g. "ba ba mu", "na na pe" etc.), and discriminate them from otherwise similar random sequences such as ABC (e.g. "mu ba ge", "pe na ku" etc.), or from one another (e.g. ABB vs. AAB) (Gervain et al. 2008, 2012).

How are these abilities encoded in the newborn brain? More specifically, is the brain specialized for language from the beginning? Studies conducted using NIRS and functional magnetic resonance imaging (fMRI) suggest that three-month-olds (Dehaene-Lambertz et al. 2002), full-term neonates (Peña et al. 2003) and even premature newborns (Mahmoudzadeh et al. 2013) activate approximately the same brain network as adults (Friederici 2012), i.e. the superior and middle temporal gyri, the inferior parietal cortex and the inferior frontal gyrus, including Broca's area, in response to language, but not to non-linguistic controls such as backward speech. As we will discuss in the Section titled 1.1. Why study newborns?, this

specialization, in particular its lateralization (Telkemeyer et al. 2009), may already be shaped by prenatal experience.

3. Speech Perception Abilities Shaped by Prenatal Experience

An increasing body of research is exploring the prenatal period, showing that fetuses already learn from the speech signal available to them during pregnancy. Moreover, several studies have shown that newborns' speech perception abilities seem to be shaped by this prenatal experience (Gervain 2015).

Starting from the twenty-fourth to twenty-eighth week of gestation, the auditory system is functional (Eggermont & Moore 2012). Fetuses thus have access to different types of sounds present in the uterus: the mother's heartbeat and respiration, sounds of digestion, of movements (Busnel & Granier-Deferre 1983) and voice (Petitjean 1989). It is thus during the third trimester of gestation that the fetuses first experience spoken language. Within this period, fetuses already show responses to speech. DeCasper et al. (1994), for instance, showed, by measuring changes in fetal heart rate, showed that fetuses react differently to a children's rhyme that was often repeated in their environment, compared with a novel rhyme. A recent fMRI study investigating brain activation in fetuses during the last trimester of pregnancy has found an activation in the left auditory cortex in response to auditory stimuli at 33 weeks of gestation. Nevertheless, the prenatal speech signal differs from the full (speech) signal available after birth. The exact characteristics of the speech signal heard by the fetuses in utero are not yet completely known. However, some studies, with both simulations and human and animal models using intrauterine recordings, have contributed important insights into this question, both with simulations as well as human and animal models using

intrauterine recordings (Gerhardt et al. 1992, Griffiths et al. 1994, Querleu et al. 1988). These studies have shown that external acoustic stimuli are mostly available to the fetus in the low frequencies, as the power of the higher frequencies is significantly attenuated by the tissues of the womb. More precisely, maternal tissues act as a low-pass filter around 400-600Hz (Lecanuet & Granier-Deferre 1993). This natural filter mainly preserves the prosody of speech (i.e. the rhythm and melody of language) but drastically reduces the finer acoustic information of speech sounds, with the possible exception of some information about certain stressed vowels (Moon et al. 2013), but no consonant information. Hence, newborn infants already perceive speech during the last three months of pregnancy, but due to the filtering effect of the womb, fetuses mainly experience speech through its prosody and it is only after birth that the fine-grained acoustic information of the speech signal becomes available to them. An increasing body of research shows that this prenatal experience already shapes the speech perception abilities of newborns at birth.

Newborns show preferences for sounds and speech stimuli they heard in utero, indicating that they can learn from prenatal experience. One such preference newborns show is for their mother's voice, compared with an unknown female voice (DeCasper & Fifer 1980; Moon 2017). Interestingly, newborns show equal preference for their mother's voice whether unfiltered (0-10 kHz) or filtered (low-pass-filtered 0-1 kHz, with frequencies between 0 and 1kHz attenuated by 6 dB and frequencies beyond 1 kHz attenuated by 48 dB), the former corresponding to the voice they hear after birth and the latter mimicking what they heard in utero (Spence & DeCasper 1987). Control newborns who were exposed to the unfiltered and filtered voice of an unfamiliar woman showed a clear preference for the unfiltered stimulus. The fact that newborns accept only the filtered voice of the mother only suggests that this preference may be conditioned by infants' low-pass filtered prenatal experience. Similarly, newborns show a preference for a melody they heard repeatedly during the last trimester of

gestation over an unfamiliar one (Granier-Deferre et al. 2011, Panneton & DeCasper 1986) as well as for a story that the mother had read aloud during pregnancy (DeCasper & Spence 1986).

Newborn infants can also discriminate their native language from a rhythmically different unfamiliar language and prefer listening to it over unfamiliar languages. Mehler et al. (1988) showed that French four-day-old newborns are able to discriminate utterances from their native language from utterances in another language (French vs Russian) and show a preference for the French utterances. Interestingly, when using low-pass filtered versions of the utterances, preserving prosodic information, newborns showed the same pattern of response. Newborns' preference for their native language was established by Moon and colleagues (1993), who presented English and Spanish utterances to Spanish and English twoday-old newborns. Using a preference procedure that presented auditory stimuli contingently on newborns' sucking behavior, the authors showed that Spanish newborns prefer listening to Spanish utterances and English newborns to English utterances. The case of the bilingual newborns is also of interest here. Byers-Heinlein and colleagues (2010) documented that bilingual newborns whose mothers spoke both English and Tagalog during pregnancy were able to discriminate the two languages, while showing equal preferences for both of them. This means that, already at birth, bilingual newborns have a sufficiently detailed representation of the two languages they heard in utero to allow them to distinguish one from the other as long as they are rhythmically different.

In line with these findings, an increasing and exciting body of research suggests that this prenatal experience could shape in even more specific ways newborns' speech perception abilities in even more specific ways and could lay the foundations for subsequent language acquisition. Specifically, several studies provide evidence that newborns learn about the distinctive prosodic features of the language(s) they heard prenatally. In four NIRS studies,

Abboub and colleagues (2016) showed that, at birth, one-to-four-day-old newborns are able to discriminate well-formed prosodic sequences from ill-formed ones only when the varying feature (duration, pitch or intensity) is contrastive in the language(s) heard prenatally. Hence, French newborns were able to discriminate sequences varying in duration (short-long, typical of French prosody, vs. long-short, absent from French and universally from most languages) (Nespor & Vogel 1986, Nespor et al. 2008) but not sequences varying in intensity (loud-soft vs. soft-loud) or pitch (high-low vs. low-high), two acoustic features that are present in the prosody of French, but do not carry contrastive prominence (Nespor et al. 2008). Interestingly, bilingual French-another language newborns, whose other language relied on pitch to mark prosodic prominence, also discriminated sequences varying in pitch. A similar sensitivity to prenatally heard prosodic patterns, has also been observed in a study where newborns were able to discriminate sentences according to their emotional valence (sadness, happiness, anger or neutrality) only when the sentences were pronounced in their native language, suggesting a prenatal shaping of the sensitivity to the prosodic variation associated with emotional expression in the language(s) heard in utero (Mastropieri & Turkewitz 1999). As prosody is mainly carried by (stressed) vowels in the speech signal, it has been hypothesized that while individual consonants are filtered out prenatally, some information about vowels may be preserved. Indeed, Moon et al. (2013) demonstrated that American and Swedish newborns, who had between 7 and 75 hours of post-natal exposure to language, already showed opposite preferences between the American vowel /i:/ and the Swedish vowel /y/. Both groups produced more high-amplitude sucks for the non-native vowel. The amount of post-natal exposure did not correlate with preference, suggesting that the results reflect the influence of the prenatal period. This preference implies that the speech signal available before birth carries some vowel information, which shapes newborns' phoneme perception abilities at birth.

Even more excitingly, the impact of prenatal learning may be so strong as to even influence even production. One study found that the communicative (i.e. non-pain related) cries emitted by the newborns follow the dominant prosodic contours of their respective native languages (Mampe et al 2009). The authors found that the melodic contour of the cry patterns of French and German newborns differed and that each group showed patterns reflecting the speech prosody of their native language, that is, prominence-initial in German and prominence-final in French. While the statistical analyses in this study were criticized (Gustafson et al. 2017), in subsequent work, a machine learning algorithm successfully classified newborn cries from three different languages (Manfredi et al. 2019), suggesting that the cries are sufficiently discriminable. Further work is needed to firmly establish the impact of prenatal experience on production, but if it is confirmed, it constitutes particularly strong evidence that attunement to the native language starts in utero.

In parallel, neuroimaging studies also provided evidence for prenatal modifications of the neural circuitry for speech and language processing. One issue that has received particular attention is the early hemispheric specialization of the brain for language. At three months of age, the brain activity of infants in response to sentences in their native language recruits similar left hemispheric regions as in adults, including the inferior frontal areas, superior temporal gyrus and the angular gyrus (Dehaene-Lambertz et al. 2002). In a NIRS study conducted with Italian neonates aged two-to-five days, Peña and colleagues (2003) confirmed that the left lateralization was already present at birth. They recorded the brain activity in the left and right temporal areas in response to three conditions: (a) Italian infant-directed utterances, (b) the same utterances played backwards, thus suppressing the linguistic nature of the stimuli while preserving their acoustic properties; and (c) silence. The results showed significantly greater activation in the left temporal areas in response to speech, compared with backwards speech and silence, suggesting an early dominance of left regions for the

processing of speech. A left hemispheric dominance was also observed for speech when compared with music (Kotilahti et al. 2009). Interestingly, subsequent studies showed that this early cortical network, and in particular the left lateralization, was at least partly a result of prenatal experience. In their study, Peña and colleagues presented speech to newborns in their native language. In a later NIRS study, Sato and colleagues (2012) tested Japanese newborns using a similar paradigm. The newborns were presented with Japanese played forward and backward, as well as with an unfamiliar language, English, also played forward and backward. For the native language, Japanese, as in Peña et al. (2003), the newborns showed a left hemispheric dominance for the forward as compared with the backward sentences. Surprisingly, however, no asymmetry was found between the forward and backward presentations of the unfamiliar language, English, for which responses were bilateral in both presentation directions. Another study by May and colleagues (2011) provided somewhat different results. In this experiment, English newborns listened to English and Tagalog sentences, presented forward and backward. While the familiar and the unfamiliar language induced different brain responses, with an overall advantage for the native language, the authors did not find a left lateralized advantage for forward-going speech in English. Rather, activation was similar in the bilateral temporal regions for both languages. The authors suggested that the absence of lateralization may be related to differences between the stimuli, which were low-pass filtered in May et al. (2011) but not in Peña et al. (2003). Subsequently, May et al. (2017) also tested non-filtered stimuli in two NIRS studies that probed the role of experience. First, they compared forward and backward English, the native language, and Spanish, a rhythmically different unfamiliar language, and observed the expected left-lateralized advantage for forward over backward speech in the native language, but comparable bilateral responses to the two directions in the unfamiliar language, similarly to Sato et al. (2012). In a second experiment, exploring the specificity of the newborn brain's preparedness for language, the authors compared Spanish, unfamiliar to the infants, with Silbo Gomero, a whistled language based on Spanish. This communication system, used by shepherds on the island of Gomera, is processed in the language areas of the brain in those adults who are familiar with it, but not in those who are not. May et al. (2017) explored whether the newborn brain starts out with the potential to process whistle as language and loses this ability in the absence of experience, or whether the newborn brain is more specifically tuned to speech and only learns to process whistle as language only when exposed to it. The results pointed to the second option. Newborns showed an increased and leftlateralized response to forward Spanish, but essentially no response to Silbo Gomero, suggesting that the brain's initial specialization does not extend to whistle. Interestingly, the unfamiliar language Spanish gave rise to a bilateral response, with no forward-advantage when contrasted with the native language English, but a left-lateralized response with an advantage for forward speech when Spanish was compared with Silbo. This implies that context effects may also play a role in how the newborn brain processes speech. An additional factor that influences the localization of the responses may be the acoustic properties of the stimuli, in particular for the non-native language. May et al.'s (2011) results with the low-pass filtered stimuli also point in this direction. Additionally, while observing the same leftlateralized forward advantage for the native language, French, as other studies, Vannasig et al. (2016) found right-lateralized activation for the forward unfamiliar language, Arabic. The lateralization issues notwithstanding, all studies found differences in the brain responses to the native language as compared with unfamiliar languages, supporting the view that prenatal experience shapes the early language cortical network.

One interesting question is: What properties of the prenatal signal drive the brain specialization for the native language? Specifically, is it simply having experience that matters or does the low-pass filtered nature of the prenatal signal play a role? While we do not

currently have a definitive empirical answer to this question, one NIRS study (Bartha-Doering et al. 2019) comparing responses to forward and backward speech in the native language in full-term newborns and in preterm newborns tested at term age suggests that the quality of the experience may be crucial. In this study, full-term newborns showed a left-lateralized advantage for forward speech, like in all previous studies with non-filtered stimuli, but preterm infants showed no such advantage. Since they were otherwise healthy and they were tested at term age (i.e. they had as much experience with language as their full-term peers at test) but this experience was not low-pass filtered but rather full-band, this result suggests that missing out on the prenatal signal may be detrimental. Other studies with older infants, who were born pre-term, seem to support this view, as these infants typically show language delays for aspects of language that are related to prosody (e.g. Peña et al. 2010), but less often show delays for linguistic units that are only experienced postnatally, such as phonotactics (e.g. Gonzalez-Gomez & Nazzi 2012). Phoneme perception itself may also be delayed (Peña et al. 2012). Since some stressed vowels may be perceived in utero, further research is needed to better understand how the perception of different phoneme classes patterns (i.e. is delayed or not) and assess whether the observed pattern of results are compatible with the current hypothesis. This hypothesis needs further empirical confirmation, but existing data seem to suggest that as far as prenatal experience is concerned, less is more, that is, the impoverished, prosody-only nature of this signal may be just the right kind of input for the developing auditory and speech perception abilities of the fetus.

4. Discussion: Novel Perspectives and Open Questions

Newborns show impressive universal, broad-based speech perception abilities at birth, which enable them to learn any language(s), even if those are different from the one(s) heard prenatally, as adoption studies demonstrate (Pierce et al. 2014; Ventureyra et al. 2004).

Moreover, an increasing body of knowledge shows that fetuses already learn from the speech signal heard in utero during the last trimester of pregnancy. This prenatal experience with speech shapes perceptual abilities and newborns already show some specific sensitivities for the language(s) heard in utero. The prenatal speech signal consists predominantly of low frequencies due to the low-pass filtering effect of maternal tissues. Therefore, this natural filter mainly preserves the prosody of speech (i.e. the melody and rhythm of a language), and several studies have shown that newborns are already sensitive to the prosodic properties of their native language(s).

We put forth a new hypothesis based on this empirical literature and on the insight that speech prosody, already experienced in the womb, is foundational for language development (Figure 1). We speculate that prosody is the cue that links genetically endowed predispositions present in the initial state with language experience during development.

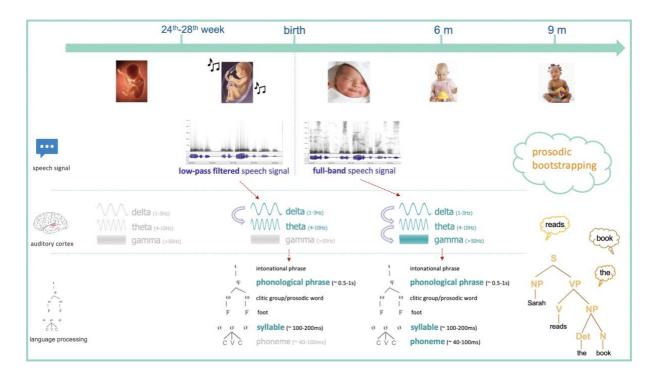


Figure 1. The prenatal prosodic shaping hypothesis.

Abbreviations: C, Consonant; Det, Determiner; N, Noun; NP, Noun Phrase; S, Sentence, V, Vowel in the linguistic hierarchy/Verb in the syntactic tree; VP, Verb Phrase. Schematic of the prenatal prosodic shaping hypothesis proposing that the speech perception system,

supported by the brain oscillations of the auditory cortex, develops through the chronological experiences of infnats with speech, starting prenatally, with prosody as the crucial cue guiding speech perception and further language development.

At the heart of this hypothesis lies the theory of embedded neural oscillations, an influential model of speech perception in adults (Ghitza 2011; Giraud & Poeppel 2012). This model emphasizes the close correspondence between the various linguistic units appearing at different time scales in speech (Gervain 2018; Nespor & Vogel 1986; Selkirk 1986) and brain oscillations operating at different frequency bands. By matching the specific temporal scales of the different linguistic units, the neural oscillations contribute to the parsing of the incoming speech into its constituent units, thus allowing the processing of speech (Figure 2). Three frequency bands are responsible for processing: delta oscillations (1-3Hz) match prosodic phrases, theta oscillations (4-8Hz) correspond to syllables and low-gamma oscillations (>50Hz) match (sub)phonemic units (Giraud & Poeppel 2012). These different brain oscillations are hierarchically nested, i.e. the faster oscillations are embedded in the slower ones. This phase-amplitude coupling between the different frequency bands (Buzsáki 2006) has been linked to cognitive performance and speech perception (Goswami 2020, Ladányi et al. 2020). Additionally, the beta band (12-25 Hz) has more recently been shown to contribute top-down information, that is, predictions for upcoming linguistic content on the basis of the listener's linguistic knowledge (Fontolan et al. 2014, Hovsepyan et al. 2020).

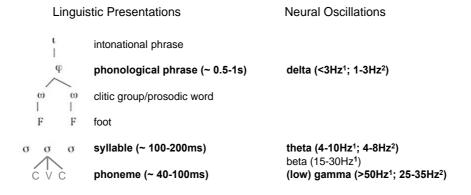


Figure 2. The prosodic hierarchy and the corresponding neural oscillations.

Representations of the different linguistic units contained in speech, hierarchically organized and embedded and the corresponding neural oscillations allowing their sampling in the context of speech perception.

Linking what we know about newborns' speech perception abilities and this neural model of speech perception, we speculate that the oscillatory hierarchy emerges from a unique developmental chronology of infants' language experience, which starts already during prenatal life. During the last trimester of pregnancy, fetuses' experience with low-pass filtered speech, which mainly preserves prosody, contributes to the attunement of the slower oscillations, delta and theta, to the prosodic properties of the native language. After birth, infants start to experience the full-band speech signal that contains the finer acoustic details necessary for the discrimination of speech sounds present in the native language. After several months of exposure to this complete speech signal, gamma oscillations, responsible for phoneme perception, are fine-tuned and get embedded in the slower already native-like delta and theta oscillations. The developmental chronology of experience with language - first the filtered prenatal signal, followed by the full-band postnatal signal - corresponds to the oscillatory hierarchy in the auditory cortex.

Our hypothesis is that prosody, the highest element of the hierarchy in which the others are embedded and the first linguistic information available to infants, guides speech perception and language acquisition. Indeed, the bootstrapping role of prosody in older infants is well established (Jusczyk 2001; Morgan & Demuth 1996; Nespor et al. 2008). Babies rely on prosodic cues to segment words (Shukla et al. 2011) or to determine the basic word order of their native language (Gervain & Werker 2013).

This hypothesis thus suggests that the prenatal period plays a fundamental role in the typical development of the speech perception system. Our study (Ortiz Barajas et al. 2021) testing newborns' and six-month-olds' ability to track the speech envelope (i.e., match theta

oscillations to the syllable rate) indeed suggests that neural oscillations in response to language are already operational at birth. Further studies are necessary to assess the presence and functions of the entire oscillatory cascade in newborns and young infants and to test their specificity for speech and language.

If empirically confirmed, this hypothesis could provide important insight into language acquisition, and it may also have important implications for atypical language development, as some children do not have a typical prenatal experience (e.g. due to preterm birth). Moreover, it could provide further knowledge about the potential links between atypical oscillatory activity in response to speech and later language impairments. Indeed, such a link has been increasingly often found in empirical studies (Ladanyi et al. 2020).

Importantly, the hypothesis does not attribute a deterministic role to prenatal experience. Prenatal experience is assumed to support subsequent language acquisition, but it is not a necessary precondition for it. During the first years of life, brain plasticity is at its maximum, and the critical period for language acquisition is open (Werker & Hensch 2015). Infants who are deprived of the low-pass filtered prenatal experience with speech (e.g., due to preterm birth or being the hearing infant of a sign mother) or whose postnatal language environment changes dramatically compared with the prenatal one (e.g., due to adoption or immigration) will develop language normally (if their postnatal experience and development is otherwise typical). Minor delays or divergences with respect to typical language development may be observed, especially early on, as discussed above. However, over developmental time, these differences diminish, and language outcomes will be within the norm.

5. Conclusion

In recent decades, great advances have been made in our understanding of how humans acquire language. Results have shown that learning begins very early, as evidenced by newborns' remarkable speech perception abilities. The development of brain imaging techniques and their applications in newborns have revealed a neurodevelopmental preparedness for language in the neonatal brain. These findings render the debate between the strictly behaviorist and nativist positions of the twentieth century obsolete. Current frameworks now conceptualize language acquisition in an interactive way, seeking to determine how innate predispositions and experience interact and lead to the mastery of a language. In this review, we presented the universal and broad-based speech perception abilities newborns already show at birth, allowing them to acquire any language. Then, we showed how these abilities are shaped by infants' experience with speech during the prenatal period, as the fetus already begins learning from the low-pass filtered speech signal available in utero during the last trimester of pregnancy. Prenatal experience is predominantly prosodic; the full-band speech signal, carrying fine acoustic information, becomes available after birth. Linking this chronological sequence of experiences with the hierarchy of the embedded neural oscillations supporting speech perception in the auditory cortex, we put forth the hypothesis that prenatal prosodic shaping is fundamental for the development of the speech perception system, laying the foundations for further language development. This hypothesis, bridges the gap between brain and behavior and provides a unified framework. The empirical investigation of this hypothesis could provide fundamental insight into speech perception and language acquisition in both typical and atypical development.

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