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Abstract

The human infant brain is the only known machine able to master a natural language and develop explicit, symbolic, and communicable systems of knowledge that deliver rich representations of the external world. With the emergence of non-invasive brain imaging, we now have access to the unique neural machinery underlying these early accomplishments. After describing early cognitive capacities in the domains of language and number, we review recent findings that underline the strong continuity between human infants' and adults' neural architecture, with notably early hemispheric asymmetries and involvement of frontal areas. Studies of the strengths and limitations of early learning, and of brain dynamics in relation to regional maturational stages, promise to yield a better understanding of the sources of human cognitive achievements.

The remarkable and complex cognitive functions observed in humans do not suddenly emerge in adulthood but are shaped by two decades of development. After centuries of considering infants' mental life as either empty or confused, research in cognitive development has repeatedly shown considerable cognitive competencies in the first months of life, despite infants' highly limited motor behavior. This set of early capacities projects human infants on a learning pathway beyond the pathways available to other animals. This pathway already bears some of the hallmarks of learning and cognition in human adults. In some domains, such as language, human infants are even better learners than adults. In other domains, such as numerical cognition, infants lag far behind adults in the extended process of developing knowledge of mathematics, but are already beginning to build a path leading from a set of core capacities shared with other animals to uniquely human, abstract knowledge. The neural architecture underlying these early capacities has long been out of reach, but this is no longer the case, thanks to the development of non-invasive brain imaging techniques permitting careful comparisons of the brain's functional architecture in human infants, human adults, and non-human animals. Such comparisons promise to shed light on the key elements underlying human cognitive achievements.

Language in infancy

Language is the paragon of human cognitive sophistication, and it is certainly from this domain that many of the best examples of human infants' early competencies can be drawn. Many of these capacities have been discovered only recently, because verbal production develops slowly: After a stage of vocalization, then babbling, human infants commonly produce their first words at the end of the first year, and they produce multiword utterances with a substantial vocabulary only at about two years of age. Carefully designed experiments have shown, however, that infants' receptive capacities are substantially better than their production and present three crucial features. First, long before any effective language production, infants are sensitive to the particular vocal sounds and combinations used by their native language to create words and sentences. They recognize their native language prosody at birth (Mehler et al., 1988) and establish the phonetic repertoire of their language during the first year of life, starting with sensitivity to the vowels of their native language (Kuhl et al., 1992) and progressing to consonants (Werker and Tees, 1984) and then to the combinations of phonemes allowed in native words (Jusczyk et al., 1994). These findings illustrate the adept and progressive analyses of the different levels of speech organization that allow infants to discover and learn familiar speech patterns.

A second line of competencies concerns infants' ability to infer the abstract structure of speech. Infants rapidly become sensitive to word categories, storing the most frequent function words of their native language by 6 months (Shi et al., 2006b) and using the higher frequency of some syllables in an artificial speech stream to parse the stream at 7 months (Bernard and Gervain, 2012). By 12 months, function words and grammatical suffixes have a different status for infants than open-class words and morphemes (Shi, 2014). Before they produce fully grammatical sentences, 24-month-old toddlers analyze the syntactic structure of sentences and display ‘‘error’’ event-related responses when the sentences are ungrammatical (Bernal et al., 2010; Oberecker and Friederici, 2006).

Finally, a third line of early competencies crucial for language acquisition has been reported: long before they speak, infants begin to connect words to the things to which they refer. Around 6 months, infants begin to understand some content words that refer to people (e.g., ‘‘mommy,’’ ‘‘daddy’’), objects (e.g., ‘‘bottle,’’ ‘‘foot’’), and action verbs (e.g., ‘‘hug,’’ ‘‘eat’’). When images of two objects (e.g., a foot and an apple) are presented side by side on a computer screen, 6-month-old infants look more to the object named by their mother in a sentence such as ‘‘Where is the X, look at the X’’ than to the other object (Bergelson and Swingley, 2012; Tincoff and Jusczyk, 1999, 2012); by the end of the first year of life, they understand about 50 words (Fenson et al., 1994). In the lab, infants associate words with visual shapes at 4 months (e.g., ‘‘bubu’’ with a curvy shape; ‘‘kiki’’ with an angular shape; Ozturk et al., 2013); by 6 months, they extract a nonce word from a sentence using prosodic and statistical cues and map it on a visual referent (Shukla et al., 2011). More generally, verbal labeling facilitates object categorization: after several exemplars of a category (dinosaurs or fishes) are presented to 3-month-old infants, the infants respond with greater attention to a new dinosaur or fish if it does not belong in the familiar category, provided that each of the familiar members of the category was accompanied by the same verbal label. Interestingly, verbal labels are more efficient in this task than tones and backward speech for these young infants (Ferry et al., 2010). Verbal labeling also aids 14-month-old infants' ability to hold representations of objects in working memory (Feigenson and Halberda, 2008). Thus, language begins early to foster human infants' processing of information about the surrounding world.

At the end of the second year, toddlers can exploit the relations between words and things to learn aspects of the grammar of their language. In one experiment (Lany and Saffran, 2010), toddlers first listened to 32 sentences composed of four nonce words (e.g., ''erd deech ush coomo'') coming from two lists. One list consisted of monosyllabic nonce words always preceded by the syllables (''ong'' or ''erd,'' e.g., ''ong deech''); the second list consisted of bisyllabic nonce words preceded by ''alt'' or ''ush'' (e.g., ''ush coomo''). Then, six different pictures of animals or vehicles were presented, such that words in each category were consistently associated with one list (e.g., animals with the bisyllabic words). The toddlers were subsequently surprised (i.e., looked longer at the image) when an image was incorrectly associated with a word from the other list (a vehicle with a bisyllabic word in our example). This was not the case in a control group, for whom the only difference was that the syllables were inconsistently associated with the mono- or bisyllabic words during the initial presentation of the sentences. Once infants learned the conditions of application of the four syllables that preceded the nonce words, therefore, they were able to match these two complementary categories to visual categories. This example illustrates the versatility of infants' distributional analyses and their fast mapping of words to objects in different conceptual domains. A similar mechanism may underlie the matching of nouns to objects and of verbs to actions, because objects and actions are conceptually distinct, and nouns and verbs have complementary associations with the specific syllables representing articles and pronouns.

Mechanisms Underlying Early Language Learning

All these laboratory experiments are conducted in a few minutes, with no pretraining. They therefore reveal competencies that are readily available for language learning and cognitive development. Two main mechanisms have been proposed to explain infants' successes: statistical analyses of speech input and sensitivity to abstract patterns. A succession of experiments, beginning with the landmark study of Saffran et al. (1996), has demonstrated infants' powerful abilities to discover statistical properties of speech and thereby to uncover the phonetic inventory of their native language (Maye et al., 2002), to segment the continuous speech stream into words (Bortfeld et al., 2005; Ngon et al., 2013; Saffran et al., 1996), to establish long-distance relations between syllables (Friederici et al., 2011; Kabdebon et al., 2015), and to infer both the grammatical categories of words (Hochmann et al., 2010; Shi et al., 2006a) and word meanings (Xu and Tenenbaum, 2007).

Some of these capacities have also been reported in animals (e.g., tamarins [Hauser et al., 2001] and rats [Toro and Tobalon, 2005]), demonstrating the universality of distributional analyses. What is remarkable in human infants, however, is the simultaneous efficiency of these analyses at different levels of the speech hierarchy and the particular combination of speech cues that young children use. For example, to construct the closed-class word category, infants must note the co-occurrence of syllables sharing specific acoustic properties (low intensity, short duration, weak stress, particular distributions of phonemes) and their reproducible positions in prosodic domains. Children also associate the statistical structure of visual objects (cf. dinosaurs in Ferry et al., 2010) with the recovery of high-frequency speech events embedded in particular frame contexts (Mintz, 2003; Xu and Tenenbaum, 2007).

The strengths and limitations of infants' statistical learning suggest how speech input is channeled in the infant brain, because the computational possibilities are framed by the neural architecture. For example, infants discover words in a speech stream only within a limited set of prosodic domains (Shukla et al., 2007) and only when statistical structure is weighted against other speech cues (Johnson and Seidl, 2009). Thus, the different levels of the prosodic hierarchy may correspond to different neural units. The superior temporal region, organized in areas of progressively longer temporal windows, is a likely substrate for this processing hierarchy (Dehaene-Lambertz et al., 2006). The precise description of the characteristics of speech statistical analyses in infants, together with increasingly realistic models of human infants' functional architecture, thus may inform models of language acquisition.

Another mechanism of language acquisition has been proposed by Marcus et al. (1999): 7-month-old infants are sensitive to the abstract pattern underlying syllable triplets. In this experiment, after a short familiarization with trisyllabic words sharing the same structure (aab, immediate repetition of the first syllable, or aba, delayed repetition of the first syllable after an intervening syllable), infants discriminated the two types of words over variation in the specific syllables presented. Because infants generalized their learning to new syllables, these findings were interpreted as showing infants' sensitivity to algebraic patterns. Subsequent research has revealed that infants' algebraic capacities might be limited at first to the detection of immediate repetitions (Endress et al., 2009), but their sensitivity to repetition can apply to abstract representations. In particular, 7-month-old infants can learn a hierarchical organization of repetitive structures (Kovacs and Endress, 2014). In this experiment, infants first listened to sentences composed of three trisyllabic words, each word being either of the type aba or abb. These words were organized in a sentence with an ABB structure, for example aba abb abb, such that the two distinct words at the end of the sentence shared the same repetitive structure. When subsequently presented with sentences in which words were now organized with an AAB structure (abb abb aba), infants detected the second-order change in the repetitive structure, looking longer to the speaker when it played the new type of sentence. Although they detected the second-order regularity only when the repeated words comprised adjacent repetition (they failed for abb aba aba sentences), this study reveals that infants have access to embedded structures during the first year of life. Once again, speech seems to have a special status, as 5-month-old infants fail to detect algebraic patterns in nonlinguistic material (e.g., tones and visual shapes) unless this material is preceded by words sharing the same structure (Marcus et al., 2007).

The ability to detect algebraic patterns associated with the use of labels for categories of objects points to the possibility that human infants might have access to symbolic representations and recursive rules. Human adults commonly use symbolic systems (e.g., speech, numbers, writing codes, algebraic formulae) to represent aspects of the external world, and we easily and flexibly map symbols to objects and vice versa. Our ‘‘symbolic minds’’ might depend on species-unique aspects of human neural architecture, in particular the expansion of associative cortical areas and the development of new long-distance fiber tracts, such as the arcuate fasciculus (Rilling et al., 2008). More efficient connections to and from the frontal lobes and longer memory buffers may lead to the discovery of more abstract structures, enabling humans to represent the external world with a symbolic system.

This possibility raises questions for studies of human brain and cognitive development. When is the maturation of this architecture sufficient to support symbolic representations in infants? At what age do infants spontaneously and efficiently use symbols to gain access to abstract concepts? Before asking whether and how the infant brain supports such symbolic functions, let us take a look at another talent shown by human infants that is deeply linked to language and symbols at older ages: numerical cognition.

Numerical Cognition

The system of natural number concepts is unique to humans (Dehaene, 2008) and likely universal across human cultures (Dehaene et al., 2008), but it is not expressed until middle childhood, at ages ranging from as low as four to as high as ten years, in research testing children in different cultures (e.g., Carey, 2009; Piantadosi et al., 2014). The roots of this system nevertheless can be discerned both in newborn human infants and in animals of diverse species. Both infants and animals represent number abstractly, albeit imprecisely. For example, human newborns who are presented a train of sequences of 4 or 12 different syllables (e.g., ba-ba-ba-ba, ti-ti-ti-ti, .) show reliable looking preferences between visual arrays of 4 vs. 12 forms: like adults who tend to look at the events we hear, newborn infants look longer at visual arrays that correspond in number to the auditory sequences (Izard et al., 2009). Because these visual and auditory arrays differed in modality, in format, and in a host of low-level perceptual variables, this looking preference provides evidence for sensitivity to abstract number.

Although the precision and robustness of number representations increase over development (Halberda and Feigenson, 2008), the numerical representations found in human infants have the same five properties at all ages. First, they are approximate and ratio limited: newborn infants' numerical sensitivity is apparent only when numerical arrays differ by a ratio between 3 and 2 (Coubart et al., 2014; Izard et al., 2009); the critical ratio progressively decreases with development in infancy and beyond. Second, they support operations of approximate addition and subtraction (McCrink and Wynn, 2004) as well as numerical ordering and comparison (Brannon, 2002) and proportional reasoning (McCrink and Wynn, 2007; Xu and Garcia, 2008). Third, these representations are linked to representations of spatial quantities, especially length, in a form that may support the universal discovery and use of number lines (Dehaene et al., 2008). For example, newborn infants are predisposed to linking increases in the number of objects in an array to increases in the length of an accompanying line (de Hevia et al., 2014). Fourth, approximate number representations form slowly and increase in speed with development (Wood and Spelke, 2005). Fifth, when infants are presented with sets of objects, representations of approximate number compete for attention with representations of the individual members of the set; when presented with small numbers of objects, representations of the individuals often win the competition (Coubart et al., 2014; Hyde and Spelke, 2009; Hyde and Wood, 2011), although they do not always do so (Starr et al., 2013b). All these signatures have been found in older children and adults as well as in nonhuman primates, rodents, birds, and fish (see Spelke, 2011 for review). Thus, representations of approximate number are present and functional throughout human development, and they depend on mechanisms whose evolution far precedes the emergence of our own species.

Starting in the third or fourth year, children begin to learn words for numbers. The process of number word learning is not well understood despite intense study (compare Carey, 2009, to Leslie et al., 2008), but it is clear that this process engages the system of approximate number representation that emerged in infancy. Although number words are used by adults to designate exact cardinal values, children's first number words elicit representations of approximate numerical meanings (Pinhas et al., 2014). Moreover, three-year-old children's mastery of number words is predictable from their performance, as six-month-old infants, in tests of nonsymbolic numerical discrimination (Starr et al., 2013a). Both adults and children solve problems of symbolic mathematics more rapidly and accurately if they first are primed by a task requiring operations on nonsymbolic numerical arrays (Hyde et al., 2014; Park and Brannon, 2013). These findings strongly suggest that our uniquely human talent for mathematics builds on ancient systems with a long phylogenetic and ontogenetic history (Dehaene, 2008).

By the age of four or five, most children in industrialized countries have mastered the mechanics of counting and the exact meanings of number words (Carey, 2009; Davidson et al., 2012; Lipton and Spelke, 2005). At about the same age, children develop a functional concept of exact numerical equality that they can apply in the absence of any number words: Presented with an array of five or six objects, such children judge that the array will change in number if a single object is added or removed but not if one object is added and a different object is removed (Izard and Spelke, 2015). In contrast, younger children judge that such an array will not change in size if the same individual element is removed and then returned to the array, but they fail to judge that it will remain the same size if one element is removed and a different element is added (Izard et al., 2014). This contrast testifies to a qualitative change in children's numerical concepts: a change that some but not all investigators argue marks the emergence of the system of natural number (Carey, 2009; Spelke, 2011; cf. Leslie et al., 2008).

The abstract notion of exact numerical equality develops hand in hand with children's developing lexicon of words for exact numbers (J. Jara-Ettinger, S. Piantadosi, E.S.S., R. Levy, and E. Gibson, in revision), suggesting that mastery of the uniquely human system of natural number concepts is linked in some way to our uniquely human mastery of a natural language. In support of this suggestion, the system of natural number has been found in every culture of the world, including cultures with a more restricted numerical vocabulary than the conventional base systems that now pervade industrialized countries (Butterworth et al., 2008; Dehaene et al., 2008). Moreover, deaf adults who have spent their lives in hearing communities, with little access to a conventional language, lack critical aspects of the natural number system, despite exposure to Arabic notation in the form of money and measurement devices (Spaepen et al., 2011, 2013). Nevertheless, these studies do not reveal the role played by language in the emergence of natural number concepts or the process by which those concepts develop.

We have focused on one case of human cognitive development, but infants have remarkable abilities to gain knowledge in diverse domains. Beginning at birth, they represent and learn about objects and their mechanical interactions (Baillargeon, 2004; Stahl and Feigenson, 2015; Valenza et al., 2006), biological motion (Simion et al., 2008), people (Gliga and Dehaene-Lambertz, 2007) and their actions and goals (Gergely et al., 2002; Saxe et al., 2005; Woodward, 1998), and about abstract entities including numbers (Brannon, 2002; Xu and Spelke, 2000), geometrical forms and relations (Lee et al., 2012; Lourenco and Huttenlocher, 2008), probabilities (Te´ gla´ s et al., 2007; Xu and Garcia, 2008), communication (Powell and Spelke, 2013; Vouloumanos et al., 2014), and mental states (Kova´ cs et al., 2010). In all these domains, the development of knowledge begins in early infancy and unfolds in a regular pattern thereafter, converging on uniquely human systems of knowledge that are explicit, symbolic, and communicable to others.

The Promise of Studies of Infant Neural Architecture

To summarize, human infants are able to manipulate different levels of speech and naturally link word units to conceptual units. They also are able to form concepts that develop, over the preschool years, into systems of abstract knowledge that are unique to humans. Finally, infants' language and systems of knowledge develop in synchrony and appear, in many cases, to be closely intertwined. What leads humans, and only humans, on this developmental path?

Although behavioral studies have brought important insights into infants' early capacities, they provide only limited answers to the question of why only humans develop systems for expressing abstract concepts that are productive, explicitly communicable, and symbolic. Almost all of the capacities described in young human infants have been reported in animals, prompting enduring disputes over the sources of our unique achievements. These quarrels miss the point that the human infant brain is the only known machine able to efficiently master a natural language, and to develop systems of knowledge such as the natural numbers, over just four or five years of life, prior to any formal instruction. Careful study of the neural bases of human infants' cognitive achievements promises to shed light on the specific neural architecture that supports this set of competencies and developments, providing new solutions to this old problem.

We are just at the start of this research and have gained only limited information, because it remains difficult to image infants as they engage in a cognitive task. These difficulties stem in part from the low compliance of young subjects, the impracticality of studies involving extensive training of infants, and the impossibility of giving verbal instructions. Further difficulties arise from the small size and immaturity of the infant brain, which affects the characteristics of MRI images and of electrical activity. Today, we are able to obtain structural and functional images of the human brain from the first stages of cognition, in prematurely born infants and even living fetuses, with magnetoencephalography (Draganova et al., 2005; Muenssinger et al., 2013) and fMRI (Fulford et al., 2003). Before describing the insights afforded by functional brain imaging studies, we rapidly describe structural human brain development from the last weeks of gestation to provide a first look at the available neural resources underlying infants' cognitive capacities.

A Brief History of Human Brain Development

Normal human gestation lasts 282 days (±13 days) post menstrual period (i.e. 40 wGA) but prematurely born infants may survive from 28wGA, even 23wGA, facing an increased risk of neurological and cognitive impairment (D'Onofrio et al., 2013). During the last trimester of gestation, the complex gyrification of the typical human brain (figure 1A) develops in parallel with the final migration of neurons in the cortical plate and the setting up of connectivity. The six-layered lamination of the cortex becomes fully visible after 32 wGA, and all neurons are in place at term (Burkhalter et al., 1993; Kostovic and Judas, 2010). Prenatal development in humans, as in other primates, is characterized by the expansion of the subplate zone, where migrating neurons and waiting afferent fibers establish numerous transient connections (Hevner, 2000; Kostovic and Judas, 2010). The first synapses appear in the cortical plate around 23-26 wGA, with a massive relocation of the afferent fibers from the subplate to the cortical plate from 28 to 32 wGA (Burkhalter et al., 1993; Hevner, 2000; Kostovic and Judas, 2010). A transient circuitry, critical in the organization of the cortex, is observed during this period : Thalamic afferents connect both the pioneer neurons remaining in the subplate and their target pyramidal cells in the cortical plate in order to amplify the input signal (Kanold and Luhmann, 2010). Interneurons arrive in place after the pyramidal cells they control (Marín-Padilla, 2011). Parvalbumin inhibitory inter-neurons, essential for learning

(Hensch, 2004), are not differentiated before 26wGA and develop very slowly in an inside-out pattern until at least 10 months of post-term age (Honig et al., 1996).

The last trimester of pregnancy is also marked by a fast emergence of short-range connectivity in addition to the long-range association pathways that developed since the second trimester of gestation and are clearly identified with diffusion tensor imaging (DTI)/diffusion spectrum imaging (DSI) during the 29- to 34- wGA period (Takahashi et al., 2012). In primates, feedforward cortico-cortical connectivity mainly originating from supragranular layers develops prenatally, with an already clear specificity and thus minimal elimination of axonal branches later on. By contrast, feedback connectivity, which originates from infragranular layers, is relatively unspecific, and a protracted remodeling phase refines the pattern of connections after term by largely eliminating axonal branches (Kennedy et al., 2007). Brain areas can be ordered into a processing hierarchy by measuring the proportion of connections originating from the infra and supragranular layers. Despite the prolonged pruning of feedback connectivity, this hierarchy is specified prenatally in primates, in contrast to cats and rodents (Price et al., 2006).

After term (Figure 1), the brain continues to grow considerably in size during the first two years (at a rate of about 0.4 cm of cranial perimeter per week during the first six months), with intense metabolic changes related to synapse formation and axonal growth observed across the whole brain during the first three months of life (Blu¨ ml et al., 2013). Waves of synaptogenesis widening the cortical columns, and myelination of the fibers enlarging the white matter, continue at a slower pace for over two decades in humans, with a large heterochrony between regions and systems, although synchronized phenomena may also occur to orchestrate this diversity (Lidow et al., 1991). For example, the primary visual cortex rapidly matures during the first three months of life in parallel with the myelination of the optical radiations (Figure 4A), whereas maturation in the primary auditory cortex and acoustic radiations extends over the first three years of life (Yakovlev and Lecours, 1967). Frontal areas and cortico-cortical connections continue to mature until puberty, but myelination is already observed during the first year of life in all associative regions (Figure 1C). Brain maturation is not a linear process, and the rate of attainment of mature myelination patterns varies across regions (Kinney et al., 1988). Restricting maturation to synaptogenesis and myelination is certainly too simple, as it ignores neuronal differentiation (Honig et al., 1996), neurotransmitter modulation (e.g., the switch from an excitatory role of GABA in immature neurons to its classical inhibitory role; Ben-Ari et al., 1997), and the role of the glia.

The Functional Architecture of the Developing Brain

Mature cognition relies on a set of specialized modules, massively parallel and hierarchical, that progressively integrate and elaborate features of the environment in more and more complex and abstract representations, from low-level processors within primary cortices to heteromodal processors in associative cortical regions (Mesulam, 1998). A second system of long-range connections between frontal, parietal, and cingulate regions forms a higher-level space or ‘‘global neuronal workspace’’ that interconnects these modules and maintains access to the information they provide over several seconds (Dehaene and Changeux, 2011).

How does this functional architecture arise? The popular view of human brain maturation, highlighting the faster rate of myelination and synaptogenesis in primary areas relative to higher-level areas, has favored bottom-up views of cognitive development, according to which purely sensory and reflexive infants gradually gain access to more and more abstract thoughts (as, for example, in the theory of Piaget, 1952). In contrast to this picture, research during the last decade, using functional brain imaging techniques in healthy living infants of different ages, reveals a more complex pattern of neural development. This research challenges several aspects of classical dogma and offers new perspectives on human learning and cognitive development. We outline three sets of research findings, providing evidence that (1) a complex functional organization is in place beginning at the last trimester of gestation, (2) activity in frontal areas contributes to infants’ cognitive processing, and (3) left-right hemispheric asymmetries emerge early and prominently in human brain development.

An Early Functional Organization

At 6 months of gestation in early preterms, electroencephalography (EEG) recordings consist of long periods of low voltage interrupted by bursts of high-voltage activity, called ‘‘trace alternant.’’ EEG becomes more continuous and left-right synchronized as the functional circuits become established and thalamic generators entrain the cortex from 35 wGA on (Wallois, 2010). Yet, the slow oscillations of the blood-oxygen-level-dependent (BOLD) response can already be parceled into distinct regions, and a set of functional networks with similar topographies to those of adults has been isolated in infants between 26 and 43 wGA (Doria et al., 2010; Smyser et al., 2010). These resting-state networks are not limited to primary areas but encompass the default mode and executive control networks (Doria et al., 2010). These two networks, although initially fragmented, are adult like at term. It is noticeable that many of these networks consist of strong interhemispheric correlations at a time when EEG is poorly left-right synchronized. Future studies should explore the relation between the BOLD response and neural activity at this age, especially because the maturation of the vascular system and of the astrocytes, which mediate the relation between neural activity and the vascular response, is still poorly described. In any case, these studies confirm that the human adult functional hemodynamic repertoire has its roots during the last trimester of gestation. Spontaneous activity in these networks may take advantage of this functional skeleton to orient early learning. Moreover, the large percentage of time infants spend in active sleep (40%–60% of sleep time) during the end of gestation and the first year of life might be used to explore the possibilities offered by this functional architecture (Barttfeld et al., 2015; Deco et al., 2011; Peirano et al., 2003).

Research tracking infants’ brain responses to stimulation reveals an early channeling of information along specific pathways, rather than undifferentiated activations. Mismatch/priming paradigms, in which a new stimulus is introduced after a series of repeated stimuli, are powerful tools to explore this architecture. By manipulating which feature is repeated or changed and thus when and where this change is noticed, different levels of representation can be targeted (Dehaene-Lambertz and Dehaene, 1994). Using this type of paradigm with event-related potentials (ERPs), research has revealed that infants, like adults, compute phonetic representations independently of nonpertinent acoustical features (Dehaene-Lambertz and Gliga, 2004). For example, a similar mismatch response to a change in syllables (from pa to ta) is evoked in neonates not only when the repeated syllables before the change are physically identical but also when they are produced by different speakers (Dehaene-Lambertz and Pena, 2001). Furthermore, when two different dimensions of a stimulus are contrasted, such as the speaker's voice and the linguistic value of the syllable in the auditory domain (Bristow et al., 2009) or the number of objects and their identity/shape in the visual domain (Izard et al., 2008), mismatch responses have similar electrical latencies but different topographies on 3-month-old infants' scalp, indicating that they are generated by different brain sources and thereby suggesting that the studied dimensions are coded by different neural networks.

For example, Hyde et al. (2010) presented 6-month-old infants with a succession of arrays of objects of a particular shape and number, followed by a change in object shape, number, or both. By using near-infrared spectroscopy (NIRS) to image the BOLD response, a reliable response to changes in number was observed in parietal areas in infants, relative to no-change controls and parallel to changes that were previously observed using fMRI in studies of adults (Piazza et al., 2004), and confirming the brain sources proposed from high-density ERPs in 3-month-old infants (Izard et al., 2008). Furthermore, a reliable brain response to changes in object shape was observed in occipital-temporal areas relative to no-change controls, also parallel to that observed in adults (Kourtzi and Kanwisher, 2000; Piazza et al., 2004) and 3-month-olds (Izard et al., 2008). These examples reveal both specificity in the brain systems supporting speech, number, and object processing in infants and developmental continuity in the functioning of those systems from infancy to adulthood.

Distinctive functional responses are observed from the earliest ages (Figure 2). Thirty-week gestational age preterm neonates react to a change of consonant (/ba/ versus /ga/) with a large response widely recorded with NIRS over the superior temporal and inferior frontal regions on both sides of the brain. The response to a change of voice (male versus female) is limited to the right inferior frontal region (Mahmoudzadeh et al., 2013). These results are confirmed with EEG: mismatch responses are weaker and also less mature for a change of voice than for a change of phoneme. Thus, from the first contacts with the external world, distinct features of external stimuli are processed through different networks. This channeling depends on the local computing properties of the areas and on their connectivity to sensory systems and upper regions, which we need to better understand. The particular morphology of the human auditory associative areas (larger columns [Buxhoeveden et al., 2001] and dense short-range connectivity [Turken and Dronkers, 2011]) favoring the auditory processing of temporal features might be specified from 30 wGA, explaining preterm infants' capacity to discriminate this difficult phonemic contrast.

Involvement of Frontal Regions in Infants' Cognition

Those who view development as a progressive organization and specialization of the brain from low-level to higher-level regions as the brain matures often point to the protracted development of frontal areas, which are classically assumed to be too immature to be functional in infants. One of the most important results of functional brain imaging has been to show that this view is false. Regarding myelination, postmortem data have long revealed that the frontal pole myelinates before the temporal pole (Kinney et al., 1988). Using an index of maturation based on the MRI T2-weighted image (T2w) signal, Leroy et al. (2011) reported more recently that the inferior frontal regions are more mature than the regions bordering the superior temporal sulcus, and as mature as the planum temporale (Figure 1B). Resting-state networks comprise a frontal component from the fetal period onward (Doria et al., 2010; Smyser et al., 2010), and studies using stimulation report robust activations in this lobe, even in preterm neonates (Figure 2; Mahmoudzadeh et al., 2013).

Moreover, the frontal lobes do not respond as a global whole but rather involve distinct areas depending on the task (Figure 3): for example, distinct responses to the mother's and to an unknown female voice are observed in the median prefrontal and orbitofrontal areas (Dehaene-Lambertz et al., 2010), similar to activations to familiar/unfamiliar stimuli in adults (Roy et al., 2012). Long-term memory of the prosodic contours of the native language is accompanied by activation of the dorsolateral prefrontal region in relation to the inferior parietal region, the locus of the phonological store in adults (Dehaene-Lambertz et al., 2002), whereas significant responses are measured in the inferior frontal regions when working memory is elicited (Dehaene-Lambertz et al., 2006). This huge lobe is thus parceled into distinct functional regions that play distinct roles in infants' cognition.

The early involvement of frontal regions might be crucial to explaining human learning. As proposed by Tenenbaum et al. (2011), hierarchical predictive models may simultaneously learn at different levels, if the learner is equipped with multiple embedded spaces of hypotheses. Such models are especially fast for learning abstractions from sparse data, with a faster learning curve at the higher level because they pool evidence from multiple subsystems at lower levels. This knowledge subsequently constrains lower-level processes. The proposal of rapid high-level learning with top-down consequences at lower levels may seem provocative in the context of numerous theories of child development, which is usually presented as a slow bottom-up process. An important, open question concerns whether hierarchical, parallel, multileveled learning begins in infancy.

Although current findings from brain imaging studies of infants describe frontal activations, these activations may only occur at the top of a hierarchy of processing. However, this proposal is compatible with the structural hierarchy observed prenatally in primates (Price et al., 2006), and Emberson et al. (2015) just published a study revealing that expectation of a stimulus produces top-down activations extending down to the sensory cortices of 5- to 7-month-old infants. In this study, infants were habituated to audio-visual pairs of stimuli with occasional trials in which the visual stimulus following the sound was omitted. An occipital activation was still recorded with NIRS in these particular cases, which was similar to the activation recorded when the visual stimulus was present, whereas no such activation was observed in a control group that did not receive any audio-visual pairs but only visual or auditory stimuli. Unfortunately, frontal areas were not monitored, but this study provides an initial test of the validity of hierarchical models and the role of top-down modulation in early learning.

Ultimately, we may also be able to investigate at what age conscious access to a stimulus is possible and what advantages result from this access. Even if the structural architecture is in place (Price et al., 2006; Takahashi et al., 2012; Dubois et al., 2014), its immaturity may impair an adequate flux of information to allow external stimuli to be consciously available. This question is difficult to answer without verbal report, but one workable experimental approach is to define the functional properties of the neural responses underlying conscious access in adults and then test for responses sharing the same property in infants. Several experimental paradigms in adults using ERPs have correlated the elicitation of a P300 with the verbal report of having consciously noticed a stimulus. By contrast, earlier components such as the mismatch negativity in auditory oddball paradigms are still recorded in sleep and even in some comatose patients (Bekinschtein et al., 2009). Thus, the experimental conditions generating a P300 in adults can be used to test infants' neural responses, and the functional equivalent of the P300 might operate as a proxy for the evaluation of consciousness in infants, even before term. Using this approach, a hierarchy of neural responses can already be demonstrated during the first months of life, but with notably delayed late responses, around 1 second (Basirat et al., 2014; Dehaene-Lambertz and Dehaene, 1994). These late slow waves may correspond to adults' P300. For example, Kouider et al. (2013), recording ERPs in infants who looked at faces presented above or under their visual threshold, reported two types of responses (Figure 4B). First, the P400, a classical ERP response to faces in infants, showed a linear increase of amplitude and duration with the duration of the face presentation. Second, a late slow wave was observed only for supraliminal face presentations, showing an all-or- none effect similar to the nonlinear increase of amplitude of the P300 when adults perceived masked stimuli (Del Cul et al., 2007). This response was weak, starting around 900 ms, at 5 months but was more sustained and visible from 750 ms at the end of the first year. These findings suggest that the cerebral bases of conscious access are already in place during the first year of life with a clear frontal component. We may speculate that this conscious access serves to amplify the sensory input for infants (see Emberson et al., 2015, reported above) as it does for adults (Dehaene, 2014), but at a much slower speed than in adults.

A New Dimension in Brain Architecture: Left-Right Hemispheric Asymmetries

One significant feature of the mature human brain lies in its asymmetric structural and functional organization, with language primarily dependent on the left hemisphere and social cognition on the right. In fetuses and infants, structural asymmetries are observed along two dimensions, first in the anatomy and second in the maturational calendar: the Yakovlean torque that pushes the right hemisphere above and in the front of the left hemisphere, twisting the superior temporal region, is observed in the fetal brain

(Figure 5). The larger left planum temporale (Geschwind and Levitsky, 1968) and the recently described superior temporal asymmetrical pit (STAP), a deeper segment of the right superior temporal sulcus at the basis of Heschl’s gyrus (Leroy et al., 2015), emerge in the fetal period (Dubois et al., 2008; Glasel et al., 2011; Habas et al., 2012). Because the structure of the white matter tracts alters the movement of water molecules, diffusion tensor imaging sequences can be used to study the cerebral fasciculi (Figure 1C). Two major tracts that sustain asymmetrical human functions, the cortico-spinal tract (handedness) and the arcuate fasciculus (language), have a higher left than right fractional anisotropy in adults (Büchel et al., 2004) and also in infants studied during the first trimester of life (Figure 5C) (Dubois et al., 2009, 2015; Liu et al., 2010). Because infants of this age have very poor motor and verbal production capacities, these findings demonstrate that these asymmetries are pre-existing and not caused by functional development.

The second dimension of hemispheric asymmetry concerns the developmental regional calendar: sulci usually appear one or two weeks earlier in the right than the left hemisphere (Chi et al., 1977). This structural feature, combined with a larger right hemispheric cerebral blood flow at rest (Roche-Labarbe et al., 2012) and larger right hemispheric hemodynamic responses to stimulation (Mahmoudzadeh et al., 2013), has been interpreted as an advance in development of the right hemisphere. T2w MRI signal is sensitive to the free water present in voxels. It darkens during the first year of life as myelination and the proliferation of membranes due to synaptogenesis decrease the proportion of free water in the gray matter voxels. Using this feature to quantify maturation in the gray matter at the voxel level, Leroy et al. (2011) report a faster maturation in the right relative to left superior temporal regions during the first months of postterm life (Figure 5B), but the inferior frontal region presents a reversed tendency (left frontal in advance of right frontal).

In the white matter, myelination thickens the axonal tracts and makes them more hydrophobic. It constrains water molecules to follow the fibers and thus decreases the transverse diffusivity and increases the fractional anisotropy, two parameters measured with diffusion tensor imaging MRI sequences. Once these indices are normalized by the adult values to get rid of geometrical differences between tracts, it is possible to study maturation per se and compare the left and right tracts during development. Beyond the structural differences highlighted in the previous paragraph, the left arcuate fasciculus matures faster than the right (Deoni et al., 2011; Dubois et al., 2015) (Figure 5C). Furthermore, Leroy et al. (2011) showed that maturation in the arcuate fasciculus correlates with the maturation of area 44 in the inferior frontal region and of the posterior part of the superior temporal sulcus. Because these three structures are the key elements of the phonological loop in adults, these findings complement fMRI findings showing a functional verbal working memory at 3 months of age (Dehaene-Lambertz et al., 2006). Thus, human infants benefit from a memory buffer of several seconds to process speech and other environmental events.

Do these hemispheric differences have a functional counterpart (Figure 5D)? A left advantage of the planum temporale to process speech or speech-like stimuli (i.e., containing fast transitions) is present from birth on, whereas the right temporal region is more sensitive to the spectral dimension (Dehaene-Lambertz et al., 2002, 2006, 2010; Perani et al., 2010; Shultz et al., 2014; Telkemeyer et al., 2009; Wartenburger et al., 2007). This particular sensitivity of the left posterior temporal region to fast temporal transitions is already observed at 6 months of gestation (Mahmoudzadeh et al., 2013), that is, at the onset of the cortical circuitry, suggesting a strong genetic influence on these hemispheric functional biases. Gene transcription analyses have revealed transient asymmetries in gene expression in the perisylvian areas before 19 wGA (Johnson et al., 2009; Sun et al., 2005). In adults also, genes with a neuronal expression are asymmetrically expressed notably in the superior temporal region (Karlebach and Francks, 2015). Regional patterning of gene expression is established at birth in rhesus monkeys, and thus probably in humans. Indeed, in human fetuses, Johnson et al. (2009) have underlined the particular genetic pattern of the perisylvian areas, clustering together areas that are subsequently involved in language and speech processing in the superior temporal, inferior parietal, and inferior frontal regions.

Other functional asymmetries have been described, in particular concerning numerical cognition. The intraparietal sulcus is the main activated region observed in adults manipulating quantities (Dehaene et al., 2003), and lesions to this area impair numerical competencies both in adults and in preterm children having suffered from anoxic lesion (Isaacs et al., 2001). Interestingly, parietal responses in adults are biased to the right hemisphere when nonsymbolic stimuli are used and when manipulation of quantities is involved but to the left hemisphere when symbolic aspects of numbers are accentuated (Chochon et al., 1999). In 3.5-month-old infants, a model of the sources of the electrical scalp responses to a change of numerosity also reveals a right fronto-parietal network (Izard et al., 2008). The right parietal sensitivity to a change of number in a set of visual objects was further confirmed by an NIRS study in 6-month-olds (Hyde et al., 2010).

With age, the involvement of the left inferior parietal regions increases, decreasing the initial right bias, as shown by the same fMRI paradigm used in kindergarten children and adults (Ansari and Dhital, 2006; Cantlon et al., 2006; Rivera et al., 2005). Pinel and Dehaene (2010), studying a cohort of 209 adults, reported a significant colateralization of the posterior superior temporal sulcus activation during sentence processing and of the intraparietal sulcus activation during arithmetic. These observations are congruent with the hypothesis of a progressive involvement of the linguistic system in the development of symbolic number knowledge, thanks to more direct connections in the left hemisphere between an initial approximate representation of quantities in the intraparietal sulcus and the strongly left-biased verbal system. It is interesting to note that for arithmetic, infants are more lateralized than adults, refuting the classical idea of an initial equipotential brain (Elman et al., 1996).

It is still too early to understand the role of these functional asymmetries, why they have been accentuated in the human species, and why they are expressed so early in life. Published studies have only examined a few systems and have described only a few features of the structural and functional development, but already these examples underline an interesting feature of the human brain: a new left-right dimension has been added to the anterior-posterior and dorsal-ventral gradient of maturation observed in other mammalian brains. This third gradient, together with the extended period of development, provides a higher complexity of interactions between areas developing at different speeds and between these areas and the external world. It highlights how the brain is parceled in humans relative to other animals, an observation similarly underlined in studies of gene expression during brain development (Johnson et al., 2009).

Exploring the Possible Role of Maturational Tempo

To summarize, developmental cognitive scientists have demonstrated that the human infant possesses numerous and complex cognitive abilities. Brain imaging studies bolster these reports by showing an early specialization of the infant brain in specific networks computing particular representations. These networks are not limited to low-level regions but involve amodal associative areas in the frontal and parietal lobes even before term, when many neurons are still migrating to their final location. Moreover, in a given task, the set of activated regions is close to what is observed in adults: even left-right asymmetries are already observed. Thus, there is strong continuity between brain organization in human infants and adults. However, if the neural architecture is in place early on, regional differences in rates of maturation (cf. the patchy colors of the brains in Figure 1B) may strongly affect network dynamics, yielding different computational properties and behavior.

Infants are notably slower than adults but not consistently. The latency of the visual P1 increases from 300 ms at birth to 100 ms (adults' latency) around 12 weeks, whereas the late slow wave that is thought to be the infant equivalent of the P300 is far slower at the end of the first year, with a poststimulus latency of about 700–1,000 ms (Kouider et al., 2013; Nelson and deRegnier, 1992) (Figure 4). The temporal constraints within the same architecture are thus highly different in infants and adults, a dimension that is often neglected in models of development. This temporal heterogeneity between networks may explain some behavioral paradoxes in the developmental literature. For example, infants sometimes fail to respond to the number of objects in a set when the objects in the numerically smaller set are larger in size (Feigenson et al., 2002). This failure does not stem from a lack of numerical competency (amply demonstrated by numerous studies; see Numerical Cognition) but might be related to a faster computation of object size relative to number, driving the behavioral response. Consistent with this possibility, infants' number representations suffer more than their size representations under conditions of brief presentation (Brannon, 2002).

The differences in the timing of neural responses in different regions of a growing brain may shed light on impairments to children's cognitive abilities. In a parallel and hierarchical, multileveled space, in which hypotheses are constantly and gradually revised according to new evidence, representations that are computed rapidly may gain an advantage over those computed more slowly. They may be favored until maturation compensates the lag in the initially slower networks. However, because the space of hypotheses, and thus the priors, have already been modified by the previous history, the temporal configuration change might lead to different outcomes at different times. For example, the response to a change of voice at 30 wGA appears less mature than the response to a change of phoneme (M. Mahmoudzadeh, F. Wallois, G. Kongolo, S. Goudjil, and G.D.-L., unpublished data). We may speculate that the small advance in the maturational calendar favoring temporal over spectral auditory processing before term might serve to strengthen representations based on the subtle temporal features of the speech signal, before statistics on other features are taken into account. Pondering the weight of environmental features through maturational lags at precise spots of the neural architecture might be an easy way to genetically control a ‘‘growing mind.’’ The parcelization of gene expression in the developing human brain (Johnson et al., 2009) has provided evolution with multiple occasions for testing the most adapted equilibrium between the computational possibilities offered by a given neural architecture and the learning opportunities proposed by the usual species environment.

In early brain lesions, developmental disorders, and abnormal environments (e.g., sensory deficits, premature birth, etc.), the expected equilibrium is disrupted, and the space of hypotheses is shaped according to the evidence provided by the distorted input and/or distorted networks. The resulting behavior might be judged inaccurately by an external observer but it is correct given the hypotheses generated within the altered neural space, leading the child’s cognitive development away from the normal path. The developmental situation differs from that of lesions to a mature brain, where error signals can be produced by different brain areas due to the sudden lack of inputs from the damaged regions. The neuropsychological models proposed for adults should be adapted to take account of this temporal dimension. Our approach is not constructivist, for we view both human and animal cognition as determined by species-specific neural architecture. Learning is limited and favored by the local computational competencies of each brain area, by their connectivity, and also by temporal constraints in a physical organ.

Information on this dynamic architecture can be gained through careful exploration of children whose development leads away from the normal developmental path. One of the most provocative illustrations of a learning limitation due to unbalanced timing is Fattal et al. (2011), showing that a thiamine deficit during a few weeks during the first year of life is sufficient to cause later syntactic deficits at 9 years of age without global deficiency. On the 62 tested children, 56 had difficulties with syntactic structures comprising a movement. Thus, correct exposure to a normal language and the correction of the nutritional deficit (initially due to an insufficiently enriched milk formula) long before they began to produce sentences were not sufficient for the children to recover normal linguistic development.

Other examples can be drawn from comparisons of healthy preterm infants' performance to those of full-term infants either of the same postmenstrual age or with the same duration of ex utero life. In a series of experiments, Peña and colleagues showed that the loss of sensitivity to suprasegmental and segmental features of a foreign language that normally occurs during the first year of life was not dependent on the duration of exposure to broadcast speech (Peña et al., 2010, 2012). In contrast, sensitivity to the phonotactic rules of the native language varies with the duration of postnatal experience (Gonzalez-Gomez and Nazzi, 2012), as do a number of visual functions including binocular perception (Jandó et al., 2012) and gaze following (Peña et al., 2014). These variations should not be viewed as inconsistent but as pertinent dissociations shedding light on how these computations are realized in vivo. They may provide crucial evidence of the elementary computational elements of human cognition.

Conclusions

Much remains to be learned about the complex circuitry that underlies early developing cognitive functions and about its dependence on maturational/genetic and environmental factors (see Box 1 for the current status of the field and Box 2 for future directions). Future research will require both methodological developments to obtain better images of the active brain in healthy infants and carefully designed cognitive paradigms. We conclude by emphasizing five points. First, humans are the only species that masters systems of explicit symbols, beginning with the words of their language. Thus, we are distinguished by our symbolic minds. The continuity between the brain architecture of infants and adults suggests that infants have the cerebral resources to develop symbolic representations across a wide variety of domains. Research in brain imaging in infants remains difficult and should be actively supported if we want to understand the symbolic functions that are so central to our human cognitive specificities and to develop adequate simulations of those functions.

Second, we need a better understanding of the central features of human cognition in adults, coupled with a distinctive set of behavioral and brain signatures that afford exploration of those cognitive processes in nonverbal organisms. With such signatures, investigators can search for similar signatures in infants, despite the characteristically longer latencies of responses in young brains. We have given several examples of the similarities between infants' and adults' responses in both behavioral and brain imaging experiments, and of the insights to which these similarities lead. As understanding of developing brain systems deepens, we expect that the critical signatures of any given cognitive function will become both clearer and more specific, enriching and deepening our understanding of human brain and cognitive development.

Third, because infants have a smaller and less educated brain with different physical properties (e.g., weak myelination), infants represent a crucial bridge between animal and human adult research to separate the genuine specificities of the human brain from extraneous features related to brain size, education, and culture.

Fourth, we have emphasized the role of research in adult cognition and brain function in elucidating the early development of these functions, but the reverse relationship is equally important: an understanding of adults' cognitive capacities and brain functions will be illuminated by studies of early development. For example, long-standing motor theories of speech, and more recent theories of embodied cognition, are challenged by findings of the early perceptual capacities of human infants. More positively, studies of cognitive functions that emerge in infancy and that contribute to later cognitive achievements shed light on the nature of those achievements, the mechanisms that subserve them, and the pathways through which they arise.

Fifth, improving education remains a challenge to allowing healthy individuals to obtain full advantage of their possibilities and to help the 10%–20% of children suffering from developmental cognitive impairments. Our societies cannot leave behind such an important percentage of children, in a world in which adults' professional and familial future is so strongly influenced by their academic achievements. All these arguments plead for a strong support of research on neural and cognitive development. We can only be surprised, if not worried, to note that none of the world's major brain projects has considered development as a major topic so far.

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Box 1 'what we know'

- A complex structural and functional architecture is visible and reacts to the external world with precise patterns of brain activation from the last trimester of gestation.
- Sophisticated cognitive functions are observed in diverse domains, with developmentally invariant signature features.
- Learning occurs throughout development at multiple, hierarchically organized levels of organization.

Box 2 'what we need to know'

- Processing depth of the infant functional architecture and the role of frontal regions in top-down learning.
- Role of language (and of the future linguistic network) in the development of symbolic representations and high-level cognition.
- Computational models of early infant cognition and learning taking into account realistic neural parameters based on brain imaging data.

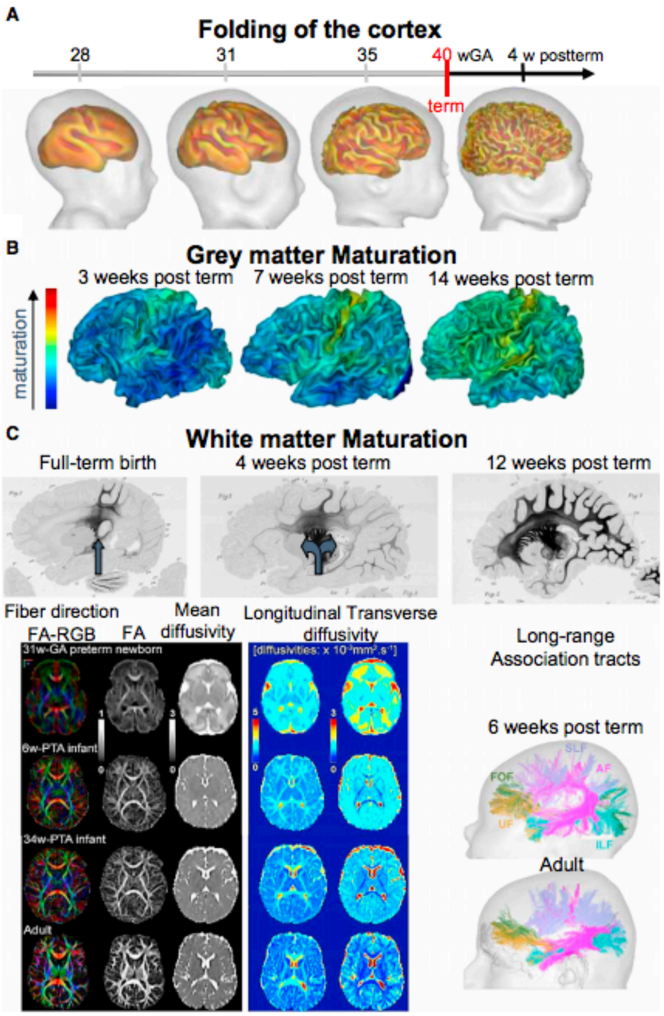

Figure 1: Images of human brain development. A) Folding of the cortex: Gyration essentially develops during the last trimester of gestation (inner cortical surfaces obtained from MR images, Dubois et al, 2008). B) Gray matter maturation. The normalized T2w signal is projected on 3D reconstructions of the inner surface. The primary areas (central sulcus, Heschl's gyrus and occipital pole) are the most mature areas (yellow). Note that the inferior frontal region is relatively more mature than the middle temporal region during the first months of life (Leroy et al, 2011). C) White matter maturation. Myelin stain in post-mortem brains (Flechsig 1920) illustrates the progression of myelination of tracts during the first trimester (first row). On the left, axial diffusion tensor images (DTI) obtained at different ages. Diffusion tensor imaging provides several parameters sensitive to myelination. Myelination decreases diffusivity, notably transverse diffusivity (the white matter becomes darker and bluer), and increases

fractional anisotropy (FA, the white matter becomes whiter). The direction of the main tensor eigenvector is coded in colour (red: right-left, green: antero-posterior, blue: inferior-superior). On the right, tractography of long-range association tracts in a 6-week-old infant and an adult reveals similar architecture at these ages (Dubois et al, 2014).

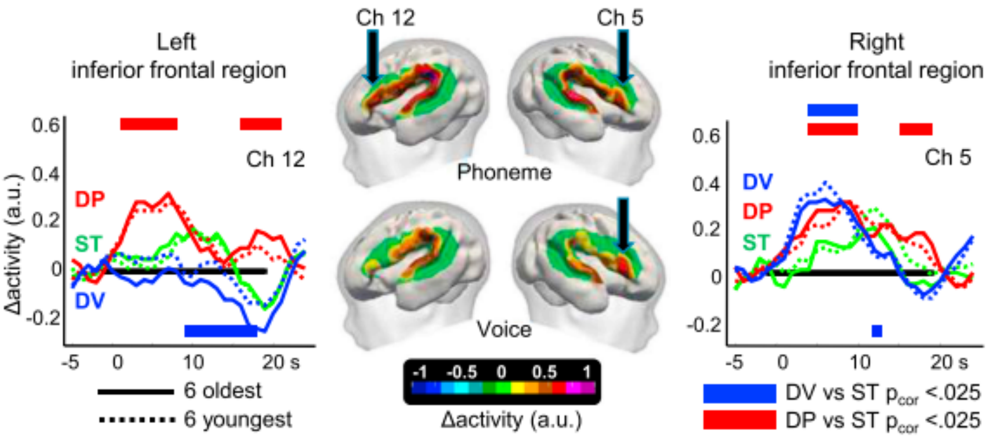

Figure 2: Preterm brain organization. Oxyhemoglobin responses to a change of phoneme and a change of voice in 30wGA preterm neonates, measured with NIRS. The syllables were presented in alternating blocks of 20 sec (black rectangle) followed by 40 sec of silence. In standard blocks (ST), the same syllable was repeated and in deviant blocks, a change of syllable occurred 3 times (phoneme, ba to ga, in DP blocks and voice, male to female, in DV blocks). The left inferior frontal region responded only to a change of phoneme whereas the right responded to both changes. The colored rectangles represent the periods of significant differences between the deviant and the standard conditions in the left and right inferior region (black arrow) (Mahmouzadeh et al, 2013).

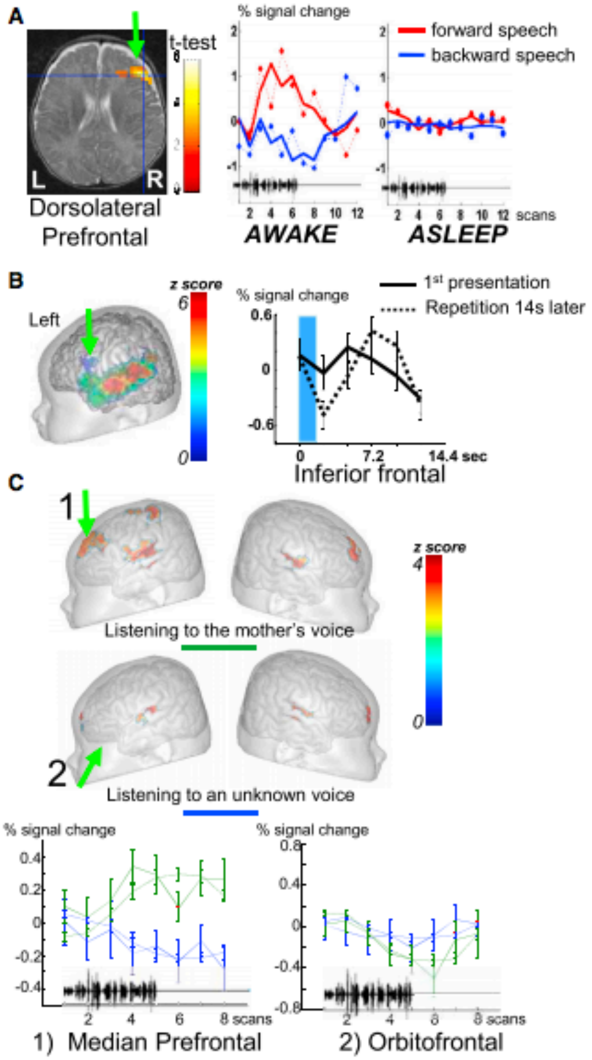

Figure 3: Frontal activations in 2-3 month-old infants. Different frontal areas are activated depending on the task. A) A stronger activation is recorded in right dorsolateral prefrontal regions when awake, but not sleeping, infants listen to their native language (Dehaene-Lambertz et al, 2002). B) Activity increases in Broca's area when a short sentence (blue rectangle on the plot) is repeated (Dehaene-Lambertz et al, 2006). C) fMRI responses to the baby's own mother's voice (green line in the plots) or to an other mother's voice (blue line). The median prefrontal and the orbitofrontal regions showed significant differences between the voices but in opposite directions, congruent with adults' responses to familiar/unfamiliar stimuli (Dehaene-Lambertz et al, 2010).

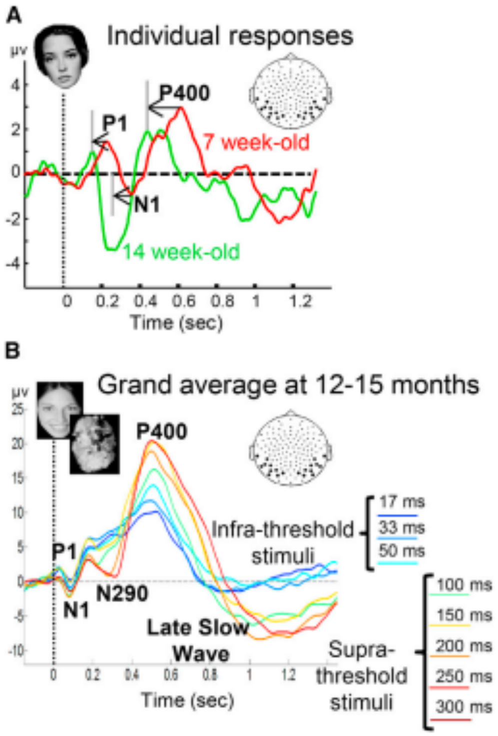

Figure 4: **Age effect on ERP latencies**. The latency of the visual N1P1 accelerates during the first weeks of life due to the rapid maturation of the visual system, illustrated here by the responses to faces in two infants recorded on the lateral posterior electrodes (A) whereas higher-level responses remain slow, even at the end of the first year (B). Because of their functional properties, the N290 and P400 are considered as equivalent to the adult N170 and the late slow wave of the adult P300. In this experiment, in which masked faces were presented to 12-15 month old infants, the amplitude of the P400 varied linearly with the duration of the face presentation whereas the late slow wave showed a non-linear response depending on the visibility threshold, interpreted as the neural signature of conscious access to the visual stimulus (Kouider et al, 2013). The heterochrony in neural processing is one of the main differences between infant and adult cognition.

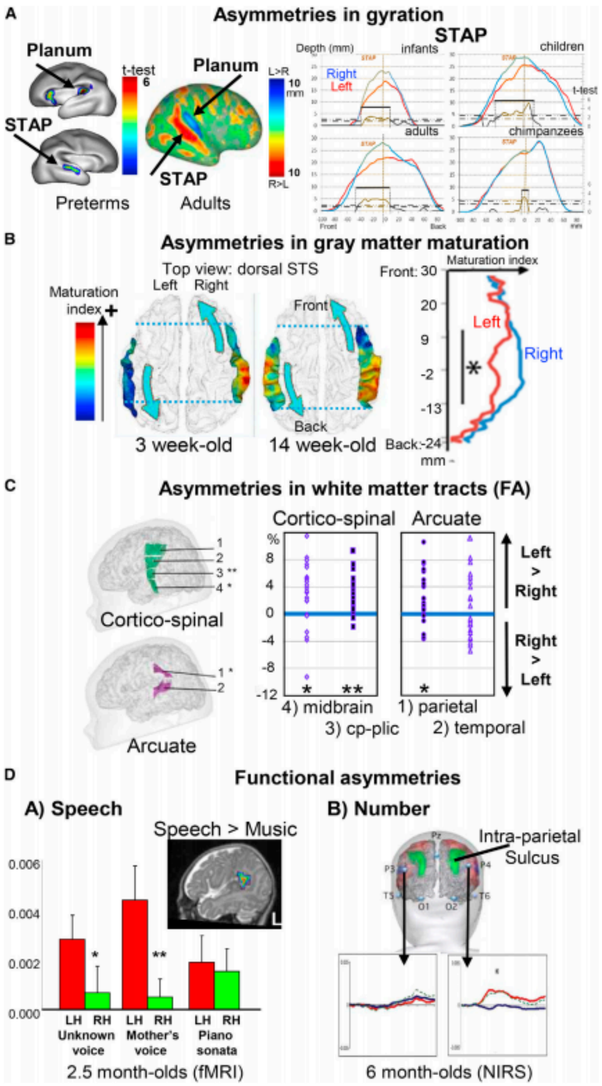

Figure 5: Early asymmetries. A) The human brain typical macrostructural asymmetries, notably a larger left *planum temporale* and a deeper right temporal sulcus (called STAP), are observed beginning in the fetal period (from Dubois et al, 2010; Li et al, 2013 and van Essen, 2005). B) The torque pushing the right hemisphere above and front of the left (blue arrows) can be seen on the dorsal view of the two individual infants' brains. The maturation of the right hemisphere is generally faster than the left during the first trimester of life as can be seen here in the superior temporal sulci and on the average index of maturation of the same structure plotted in the right column. These measures are based on the normalized T2w signal, which darkens as the free water decreases (Leroy et al, 2011). C) Fractional anisotropy (FA) increases with the

myelination/compactness of the tracts. It is higher in the left lower part of the cortico-spinal tract and in the parietal part of the arcuate fasciculus relative to the right during the first trimester (Dubois et al. 2009). D) Activation by speech is higher in the left than right *planum temporale* whereas it is symmetric for music (Dehaene-Lambertz et al, 2010). The response to a change of number in a set of objects measured with NIRS is observed only in the right parietal region in 6-month-old infants (Hyde et al, 2010).

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