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Nature and nurture in language acquisition: anatomical and functional brain-imaging studies in infants

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Speech processing in adults relies on precise and specialized networks, located primarily in the left hemisphere. Behavioral studies in infants indicate that a considerable amount of language learning already takes place in the first year of life in the domains of phonology, prosody and word segmentation. Thanks to neuroimaging, we can move beyond behavioral methods and examine how the infant brain processes verbal stimuli before learning. These studies reveal a structural and functional organization close to what is described in adults and suggest a strong bias for speech processing in these regions that might guide infants as they discover the properties of their native language, although no evidence can be provided as yet for speech specificity of such networks. This review is part of the *INMED/TINS* special issue *Nature and nurture in brain development and neurological disorders*, based on presentations at the annual *INMED/TINS* symposium (http://inmednet.com/).

Introduction

Human language achieves efficient communication based on precise mapping between sounds and meaning that is shared by all members of a group. The power of this communication tool is based on elementary bricks that can be combined in multiple ways to convey new meanings. These elementary bricks (phonemes, syllables and words) are realized as a continuous speech signal that should be correctly segmented by the listeners to decipher the information. Most human brains easily perform these complex operations in their left perisylvian regions. Why does language processing rely on these precise brain regions? Do they possess special properties that can explain language emergence in humans? Study of the cerebral bases of language processing in adults points to structural and functional differences between hemispheres, but the long-term training of adults with such stimuli makes it unclear whether these asymmetries are the cause of language development in our species or only consequences of heavy exposure to the particular acoustic properties of speech. Comparative studies aim to differentiate between the linguistic capacities specific to humans and those shared with other animals. However, similar performances do not necessarily imply both the same strategies and neural correlates. We propose that infant studies, and particularly brain-imaging studies of infants' linguistic competences, might contribute to a reappraisal of the issue of language development in our species. Such studies should reveal what human brains before intense exposure to speech have in common with the brains of animals and with those of mature and linguistically competent human adults.

Structural asymmetries in the human adult brain: a basis for speech processing?

Since Broca's seminal publication [1], numerous studies in neuropsychology and neuroimaging have associated speech processing with the left perisylvian regions in most humans, and have questioned whether a particular organization of this part of the brain might explain the language faculty in our species. Indeed, structural asymmetries are observed at the macroscopic and cytoarchitectonic levels, such as a longer left sylvian fissure and a larger left planum temporale [2], and less frequently a larger left inferior frontal region [3]. The white matter volume underlying Heschl's gyri is larger on the left than on the right side [4]. Bigger pyramidal cells are noted in the left auditory cortex [5], and these are associated with thicker myelinated fibers [6]. Widths of individual cortical columns, and distances between those columns, are greater in the left superior temporal lobe [7]. It was argued that these structural features might enable the left hemisphere to code the rapid and complex acoustic transitions characterizing speech more accurately than the right [8,9]. It thus would seem easy to attribute human speech processing capacities to these structural

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differences, especially because the planum temporale is less asymmetric in groups of speech-impaired or written-language-impaired children than in the normal population [10].

Although these structural features might indeed be particularly adapted for processing speech, a simple causal relationship between them and the language faculty might be an oversimplification. First, humans are heavily trained with speech stimuli, making it difficult to ascertain whether the observed cytoarchitectonic characteristics of the left temporal lobe are the consequence or the cause of speech processing in this hemisphere. Second, the neuronal responses in some of these regions depend more on the linguistic value of the stimuli than on their acoustic characteristics. For example, functional magnetic resonance imaging (fMRI) activations in response to phonetic contrasts, which are observed both in the posterior part of the superior temporal cortex and in the supra-marginal gyrus, depend more on the subjects' native language than on the acoustic features of the sounds [11,12]. Third, sign languages, which rely on spatial cues rather than on fast temporal cues as oral languages do, involve the same left perisylvian regions [13,14].

Brain asymmetries in animals

Another reason to doubt a strict causal relationship between brain temporal asymmetries in humans and the development of language is that the asymmetries are not restricted to human brains. Great apes also exhibit a larger left *planum temporale* [15,16], although cytoarchitectonic differences between both hemispheres are less salient than in humans. For example, the lateralization of the organization of minicolumns observed in human temporal cortex has not been found in chimpanzees and rhesus monkeys [17].

As in humans, these asymmetries are not only structural but also functional. Asymmetric electrophysiological responses are recorded in the thalamus of guinea pigs when complex sounds, such as the syllable /da/, are presented, whereas the responses are symmetric in the case of simple tones [18]. Free-ranging rhesus monkeys [19], sea-lions [20], mice [21] and harpy eagles [22] orient the right ear to a loud-speaker playing vocalization of their own species. Macaques loose the ability to discriminate two forms of their 'coo' vocalization after a left superior temporal lesion but not after a homologous right lesion [23]. This functional asymmetry was recently confirmed by a positron emission tomography (PET) study showing left-lateralized activation of the temporal poles when monkeys hear own-species vocalizations [24]. As in humans, asymmetries seem to be linked to the communicative salience of the vocalizations rather than to their acoustic parameters [21,25]. This asymmetry develops along with exposure and is not seen in infant rhesus monkeys [19] and infant sea lions [20], and in harpy eagles the active experience of hunting modifies the initial left-side bias in response to the call of a prey towards the right side [22]. Lateralization appears thus to be less unusual than previously thought, probably because it provides a superior brain efficiency for crucial stimuli. However, the interplay between hemispheric differences in acoustic processing of temporal information and/or computation of sound meaning is still not clearly understood, even in animals.

Speech processing in animals

If brain asymmetries are not unique to humans, what about processing of the speech input? One main characteristic of phoneme perception in humans is to be categorical and normalized across different acoustic realizations. Similar properties have been observed in animals. Monkeys [26], chinchillas [27] and even birds such as quails [28] can be trained to perceive speech syllables categorically as humans do, and are able to generalize this behavior to exemplars to which they have not been previously exposed. However, in addition to clear differences between species concerning the length of training necessary to obtain comparable performances, animals do not always use the same cues as humans, at least not the same ones as adult humans [29,30], suggesting that speech representations are specific in human adults. For example monkeys, but not humans, have more difficulty in discriminating /b-d/ when these consonants are followed by /i/ and /e/ than when they are followed by /a/ and /u/ [31]. The monkey performance could be explained by a general auditory mechanism computing the direction of the second formant. This direction is clearly different if /b/ and /d/ are followed by /a/, but is more ambiguous for /bi-di/ because the realization of the consonant is affected by the anticipation of the articulatory movement needed to produce the vowel (coarticulation). The difference between a speech and a non-speech mode of perception in humans is clearly illustrated when sine-wave stimuli, which can be perceived either as electronic noise or as speech, are used. Along a /ba/ /da/ continuum, the location of the boundary between the speech and non-speech mode of perception differs by one step [32]. Furthermore, perceiving these stimuli as speech correlates with activations in the posterior part of the left superior temporal region and in the supra-marginal gyrus [33], suggesting distinct phonetic representations for speech stimuli, at least in the adult brain.

More recently, comparative studies have turned to another linguistic capacity, namely the capacity to discriminate utterances extracted from different languages. Rats trained using either natural or synthesized sentences (keeping only prosodic information) in Dutch and Japanese can discriminate between these languages when they listen to new synthesized utterances or to new natural sentences produced by the same speakers [34]. However, they are unable to generalize to new speakers. Tamarins do not need training and spontaneously discriminate between these languages even when the speakers are unknown and varied [35,36]. These discrimination capacities are nevertheless limited to languages belonging to different rhythmic families (e.g. Dutch versus Japanese, or Polish versus Japanese); tamarins fail to discriminate English from Dutch, which are two stress-timed languages. Both tamarins and rats also fail to discriminate between different rhythmic families when the utterances are played backwards. Spontaneous computation of speech rhythm is thus possible in other mammals, and can be performed only on utterances that unfold naturally, respecting human production constraints. However, rats are less able than tamarins to extract language rhythm properties when too much variation is introduced by speakers' idiosyncrasy.

Infants' early capacities to process speech

Although human speech production does not become significant before the end of the first year of life, infants display early sophisticated perceptive capacities that are rapidly modified by their linguistic environment. Neonates can discriminate between languages belonging to different rhythmic families [37,38], as rats and tamarins do, but they clearly prefer to listen to their native language even when speakers are unknown [37,39]. Two-month-old infants orient faster to the speaker playing utterances in their native language than the one playing foreign sentences [40]. At ~4 months of age, they become able to discriminate their native language from languages belonging to the same rhythmic class, such as Catalan from Spanish [41] or US English from UK English [42]. In addition, infants can discriminate phonemes in a categorical manner, even those not present in their native language [43]. They easily neglect non-pertinent acoustic variations, such as voice differences, to extract the correct phonetic segments [44]. This is not due to an inability to perceive voice differences, because they recognize their mother's voice [45] and discriminate between foreign voices [46].

Even though the initial speech perceptive capacities in infants seem close to those of other animals, they are rapidly modified by the linguistic environment, and at the end of the first year infants have acquired the phonetic repertoire and phonotactic rules of their native language [43,47]. They segment speech in words and become able to pair the most frequent words with objects. This is not a trivial achievement because <7% of the speech directed at children is in the form of isolated words [48] and oral languages lack precise word boundary markers, unlike written language that uses blank space to separate words. Furthermore, the same words can have very different acoustic realizations depending on factors such as speakers' different vocal tracts, emotions or speech rate, and noise in the environment. However, by one year of age (and probably before), infants have understood that the noise other people are making is made of words carrying an information that should be decoded. From a developmental point of view, this achievement must be compared with the inability of most children of this age to walk alone, which is surprising if one considers that most other mammals are able to stand up soon after birth.

A role for prenatal exposure to speech?

It is sometimes argued that the fast learning of native-language features during the first weeks of life can be explained by exposure to speech *in utero*, because hearing function develops during the third trimester of pregnancy. This exposure would have the advantage of centering the auditory environment on the mother's voice, which is largely audible above endogenous noises (e.g. those created by arterial blood flow or heart beats) thanks to the direct transmission to the fetal ear of the mother's voice vibrations, whereas other external noises, including the father's voice, are distant and filtered by the womb [49,50]. However, the predominance of the mother's voice in the fetal auditory environment would predict different behavior for a learning network to that observed: it would favor precise representations of the mother's speech productions and predict difficulties in generalizing across different speakers. In addition, the perception of some phonemic contrasts, such as place of articulation, is affected by surrounding noise. Using recordings within the uterus of a pregnant sheep, Griffiths and colleagues [51] showed that intelligibility of these phonemes was poor in the *in utero* auditory conditions. Yet neonates have no problem discriminating phonemes that differ on place of articulation, such as /pa/ and /ta/ [52]. Young infants are even able to discriminate foreign contrasts not present in their environment [43]. These observations suggest that even though some learning takes place during the last weeks of fetal life (e.g. neonates react to the maternal voice [53], to a story that the mother has read during the last weeks of gestation [54] and prefer to listen to their native language [37]), discrimination capacities at birth exceed what could have been learned from *in utero* exposure to speech only.

In summary, infants exhibit sophisticated speech perceptive capacities, such as phoneme categorization, normalization and languages discrimination. Although these capacities are also partly observed in animals, the language learning of human infants departs from that of animals within a few weeks of life. Are these different trajectories due only to the intense exposure to speech encountered by human infants? Or do structural and functional properties of the human brain help infants to take advantage of this particular environment? The recent advances in neuroimaging techniques make it now possible to study both brain structure and brain function at an early age.

Structural and functional asymmetries of the infant brain

In humans, early structural brain asymmetries first favor the right side. During the third trimester of gestation, the superior frontal gyrus, superior temporal gyrus and Heschl's gyrus are detectable on the right one or two weeks earlier than on the left [55]. However, the sylvian fissure is longer on the left and is associated with a larger left planum temporale already during fetal life [55,56]. Twin studies reveal a strong genetic influence in these areas [57], with little influence of auditory stimulation, at least at the macroscopic level. The left planum temporale and left Heschl's gyrus are larger than their right counterparts in both hearing and congenitally deaf adults [58].

During the first year of life, there is, at rest, no left-right difference in cerebral blood flow, even in linguistic regions (i.e. inferior frontal, superior temporal and plurimodal temporal-parietal regions) [59]. However in response to auditory stimuli, asymmetric responses favoring the left side are observed in fMRI and event-related potential (ERP) studies. 20-s-long speech recordings were played either normally or backwards to neonates and to three-month-old infants [60,61]. Although forward and backward speech share common segmental features (fast temporal auditory transitions and phonetic information conveyed by temporally symmetrical phonemes), backward speech violates universal prosodic rules, affecting language discrimination capacities in infants [37], as in animals. Activation in response to both forward and backward stimuli was significantly larger in the left than in the right planum temporale in three-month-old infants [61]. Although the interaction between utterances type and hemisphere was not significant, activation in this left region reached significance for forward speech but not backward speech in neonates [60] and three-month-old infants [61] (Figure 1). Thus, significant leftward asymmetry is present for speech-like stimuli from birth onwards, but without statistical evidence of any specificity for linguistic stimuli over non-linguistic ones (possibly because of lack of statistical power). Similarly, recorded ERP voltages were higher over the left hemispheres of four-month-olds than over their right hemispheres in response to tones and syllables such as /ba/ and /ga/, again with no stronger asymmetry for the linguistic stimuli [46]. More data are needed before a conclusion can be made, but these first results suggest that during the first months of life, the left auditory areas might be more reactive than the right to any sound. This bias might contribute to orientation towards the left hemisphere of processing of the most common stimulus in the infant's auditory environment, namely speech. However, if a lesion occurs, the right perisylvian areas can take over language processing that normally occurs in the left hemisphere (e.g. phonetic discrimination in infants [62], and even expressive and receptive language in older children [63]), showing that this leftward response is only a bias. Indeed, several studies have underscored the fact that language development usually remains within the normal range after early brain lesion [64], whatever the side of the lesion.

Functional continuity from infanthood to adulthood

The lateralization observed in infants is not as strong as in adults and it consolidates during development and acquisition of more sophisticated language skills [65], but the brain regions involved when infants listen to speech are nevertheless close to those observed in adults. ERPs have been used to decipher the processing of brief sounds. By subtracting the response evoked by a stimulus preceded either by itself or by another close stimulus (e.g. da da da **da** versus ba ba ba **da**), it is possible to observe a mismatch response whose topography and latency depend on the changing feature. When a series of syllables such as /ba/ and /ga/ changes in either its voice or its phonemes, mismatch responses in infants show different scalp topographies and different latencies; this suggests that, as in adults, different networks are involved in representation of the various sound features [46]. Among these

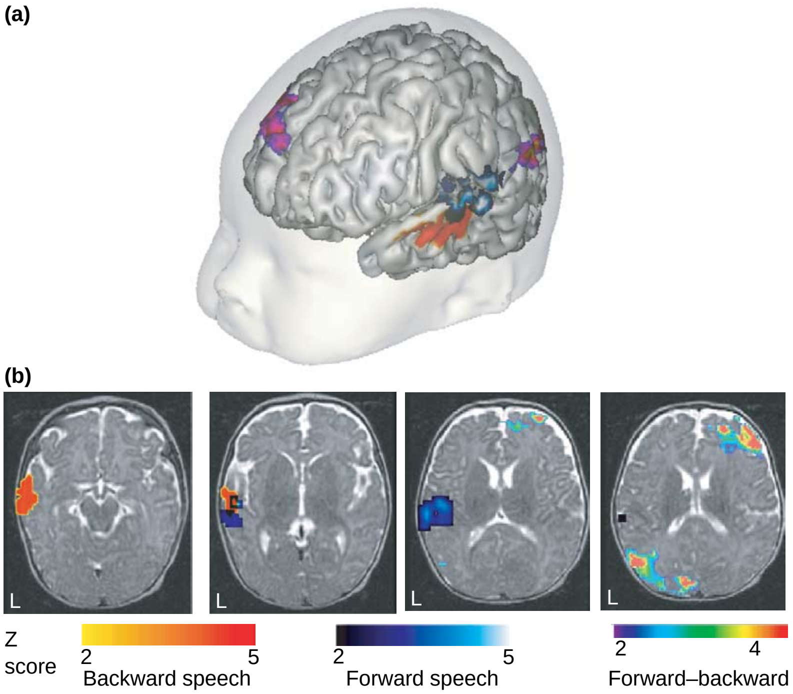

Figure 1. fMRI study of infants' speech processing. fMRI activation obtained in awake three-month-old infants listening to blocks of 20 s of normal (forward) or reversed (backward) speech relative to activity during silence are projected onto a 3D image **(a)** and axial slices **(b)** of a three-month-old human brain. From left to right the slices are taken from progressively more dorsal levels, and the front is to the top in each case. The color scales indicate the value of the *z*-score assessing the significance of the studied contrast (backward speech versus silence, forward speech versus silence, forward versus backward speech) in a random-effect group analysis at $P<0.01$ corrected for voxel extend. Activation in response to forward speech (blue scale) occurred in superior temporal regions of the brain that are dorsal and posterior to areas activated by backward speech (orange scale). However, the regions significantly more activated by forward than by backward speech are the left inferior parietal region and the right dorsolateral prefrontal regions (blue-pink scale). This figure illustrates the complex cooperation between temporal, parietal and frontal regions in the recognition of native language (forward speech). Adapted from Ref. [61].

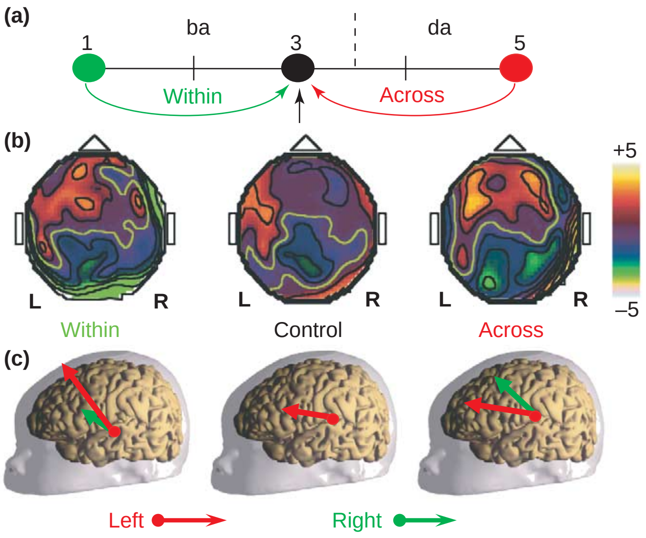

Figure 2. ERP study of infants' phonetic processing. Syllables were synthetized at equal intervals along a voiced place of articulation continuum (ba-da). Adults perceived stimuli 1 and 3 of this continuum as /ba/ and stimulus 5 as /da/. Three types of trials were randomly presented to infants while their evoked responses were recorded using 65 electrodes. In control trials, the same syllable ba^3 was repeated four times (ba^3 ba^3 ba^3 ba^3). In within-category change trials, ba^3 was preceded by ba^1 (ba^1 ba^1 ba^1 ba^3) while in across-category change trials, it was preceded by da^5 (da^5 da^5 da^5 ba^3). The physical distance measured on the continuum was similar for both changes, but only the across-category change had a linguistic value. In adults, this latter change was detected in 81% of the trials whereas the within-category change was detected only in 12.8% of the trials. This difference is due to the categorical perception of phonemes **(a)**. In infants, the voltage cartographies 454 ms after ba^3 onset were different in each condition. Both within-category and across-category changes induce a different response than repetition (control), but the discrimination response was larger and more diffuse in the case of a phonetic change (across) than of a pure acoustic change (within), demonstrating categorical perception in infants **(b)**. Moreover, dipole modeling suggested that the generators in the across-category change condition were more posterior and dorsal than in the within-category change condition **(c)**. Adapted from Ref. [66].

networks, one has been found to demonstrate phonetic properties, such as normalization across different speakers [52] and categorical perception [66]. The synchronized activity of columns of neurons that are at the origin of the scalp event-related responses can be characterized as electric dipoles. Different algorithms have been proposed to estimate what are the brain regions whose activity can account for the observed scalp topographies. Although multiple solutions of this inverse problem are possible, and the exact location and interplay of the sources in the brain remain ambiguous, source modeling can suggest interesting differences between conditions within the same experiment. Thus, a dipole modeling of the active regions coding a phonetic change has suggested that the generators were more posterior and dorsal than those involved in the detection of a similar acoustic change but without linguistic value [66] (Figure 2). This shift is compatible with the involvement of posterior temporal and inferior parietal regions during phonetic processing, as demonstrated in adults [11,33].

Box 1. Diffusion tensor MRI and tractography: a new way to explore the organization and maturation of white matter connections in the infant brain

Diffusion tensor MRI (DTI) enables imaging of the cerebral tissue structure on a microscopic scale, and probing of the spatial organization of white matter in fiber bundles [68]. Fascicles have been identified in the immature brain of newborns, either preterm or at term [69], and most of the main bundles described at later ages (commissural, projection and association tracts) have been reconstructed by tractography in the infant brain, even before maturation of these tracts is complete [70] (Figure I). Because arrangement, density and myelination of the fibers vary with age at different rates across bundles, maturation can be mapped *in vivo* through the monitoring of diffusion parameters [71]. Such sensitivity makes DTI a technique of choice for studying the development of both anatomical and functional connectivity of language networks in healthy and diseased children. It will undoubtedly enable a more precise description of structural brain asymmetries in infants, especially in the language areas as already detailed in adults [72–74].

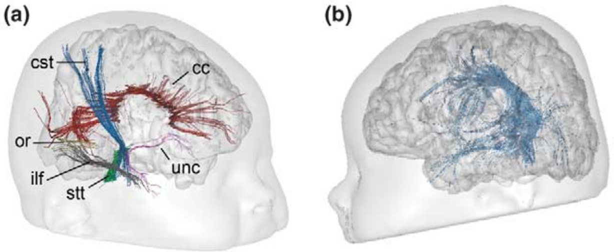

Figure I. Tractography of some major white matter bundles in the brain of a 16-week-old infant. **(a)** Shown are the corpus callosum (cc), corticospinal tract (cst), spinothalamic tracts (stt), optic radiations (or), inferior longitudinal fascicle (ilf) and uncinate fascicle (unc). **(b)** The arcuate fasciculus, a major tract involved in linguistic processing in adults, connects temporal and frontal areas.

Using fMRI in infants, responses to forward and backward sentences have been found to activate the superior temporal gyrus, encompassing Heschl's gyrus and extending to surrounding areas of the superior temporal sulcus and the temporal pole [61] (Figure 1). The angular gyrus and precuneus were activated more strongly by forward speech than by backward speech, suggesting that the angular gyrus, which is involved in lexical storage in adults, also has a role in the storage of the prosodic patterns that infants use to recognize their native language. Finally, significant activation was observed in response to forward speech in the right dorsolateral prefrontal cortex of awake but of not sleeping babies; this area of cortex is involved in memory retrieval mechanisms in adults (Figure 1). Although infants are far from possessing the refined competencies of adults, common activations in superior temporal, inferior parietal and frontal regions underscore the continuity between infants and adults.

Thus, brain regions involved in receptive speech processing in infants are not limited to unimodal auditory regions. They extend to remote regions, some of which, like the frontal regions, were considered barely functional at this age. Conversely, the infant brain does not respond to speech in diffuse areas, as connectionist models, which suggest in their extreme form an equipotential brain, would have predicted [67]. Rather, it is functionally structured, recruiting distant regions in cooperative networks. We do not know yet whether another structured stimulus, such as music, would activate the same network. However, the processing properties of the infant brain (which enable categorical perception, normalization of speech input, recognition, and long-term storage of intonation contours) make it efficiently adapted to the most frequent auditory input encountered by the human infant, namely speech.

Concluding remarks

From the first weeks of life onwards, the human brain displays normalization and phonetic categorization capacities, and rhythmic and prosodic sensitivity, which make it particularly adapted for processing speech. These capacities rely mostly on brain circuits similar to those observed in adults. It seems unlikely that the influence of the prenatal and postnatal auditory environment is sufficient to generate this complex organization in only a few weeks of exposure. On the contrary, the similarity between functionally immature infants and competent mature adults implies a strong genetic bias for speech processing in those areas. This 'bias' might partially result from recycling of auditory processes observed in other mammals (e.g. rhythmic sensitivity or perceptive discontinuities along some acoustic dimension) but is not limited to them. The functional properties of the superior temporal areas and their connectivity with remote regions in humans might be crucial to ensure language learning. For example, connections with other brain areas such as the motor or the visual system, which possess their own biases to compute conspecific representations, might be crucial for reinforcing linguistic representations and their shaping by the native language. Novel brain-imaging studies, including diffusion tensor imaging (Box 1), in infants should help to describe these networks. Although language acquisition studies have focused mostly on speech input analyses so far, a better understanding of the functional properties of the brain regions involved in speech processing in infants (e.g. preference for fast transitions, or the possibility of auditory long-term storing) might help to define the crucial parameters favoring language acquisition. These new insights will provide a strong basis for study of early developmental disorders affecting language and communication in humans.

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