Before Speech: Cerebral Voice Processing in Infants

Pascal Belin[1,*] **and Marie-Hélène Grosbras**[1]
[1]Department of Psychology & Centre for Cognitive Neuroimaging, University of Glasgow, Glasgow, Lanarkshire G12 8QQ, Scotland, UK
*Correspondence: pascalb@psy.gla.ac.uk
DOI 10.1016/j.neuron.2010.03.018

In this issue of *Neuron*, Grossmann et al. provide the first evidence of voice-sensitive regions in the brain of 7-month-old, but not 4-month-old, infants. We discuss the implications of these findings for our understanding of cerebral voice processing in the first months of life.

Vocal communication is at the heart of human life. It relies on speech perception but also on a rich set of abilities to extract, evaluate, and categorize the vast amounts of nonlinguistic information available in voices. These voice cognition abilities allow normal listeners to effortlessly identify a speaker's gender and approximate age, to recognize his/her affective state and whether or not it matches the verbal information, and include more subtle percepts such as attractiveness or trustworthiness that play a key role in our social interactions.

Voice cognition abilities appear earlier than speech perception in human development. While phoneme discrimination emerges in babies around 2 months and lexical-semantic processing around 12 to 14 months after birth (Friederici, 2005), infants show already well-developed voice perception abilities. Experiments measuring changes in heart rates in neonates during presentation of different voices demonstrate their ability to discriminate voices and to recognize the voices of their parents (Ockleford et al., 1988)—an ability even present in fetuses before birth (Kisilevsky et al., 2003).

In adults, the cerebral processing of vocal sounds is known to engage ''temporal voice areas'' (TVA) mostly located along the middle and anterior parts of the superior temporal sulcus (STS; Figure 1). Functional magnetic resonance imaging (fMRI) studies show greater activity in the TVA in response to voices (speech, but also nonspeech vocalizations such as laughs, coughs, etc.) than in response to natural nonvocal sounds (environmental sounds, musical sounds, animal vocalizations, etc.), or amplitude- or frequency-matched acoustical control sounds (Belin et al., 2000; Von Kriegstein and Giraud, 2004). The TVA also show strong sensitivity to affective information in voices (Ethofer et al., 2009; Grandjean et al., 2005) and are functionally connected to more anterior regions of the right temporal lobe during speaker recognition (Von Kriegstein and Giraud, 2004).

Voice-selective areas were recently observed in the macaque brain (Petkov et al., 2008), indicating a long evolutionary history of cerebral voice processing (Figure 2A). Comparatively little is know on the appearance of cerebral voice processing along the developmental axis (Figures 2B–2E). The earliest time point currently available on the development of cerebral voice processing is provided by a recent study using electroencephalography (EEG). The contrasts of auditory evoked potentials acquired in adults in response to auditory stimulation with vocal and nonvocal sounds highlights a ''fronto-temporal positivity to voice'' (FTPV) at around 200 ms after sound onset (Figure 2E; Charest et al., 2009). A robust FTPV has been observed in 4- to 5-year-old children (Figure 2C), suggesting that cerebral voice processing is already well established at age 4 (Rogier et al., 2010). But how does cerebral voice processing develop before age 4, at a time when speech perception is not yet operational?

In this issue of *Neuron*, Grossmann et al. (2010) bring an important missing piece to the puzzle. They used near infrared spectroscopy (NIRS) to examine cerebral voice processing in 4- and 7-month-old infants. NIRS quantifies the way cerebral tissues absorb different wavelengths of light to extract information on blood oxygenation, indirectly related to neuronal activity. The noninvasive nature of this technique is well adapted to investigations in infants.

In a first experiment, Grossman et al. (2010) examined whether voice-sensitive cerebral activity similar to that observed in adults could be evidenced. They contrasted measures of blood oxygenation acquired during stimulation with brief vocal or nonvocal stimuli taken from the ''voice localizer'' scan routinely used in fMRI studies of adult voice processing (Figure 1). Seven-month-old infants showed greater

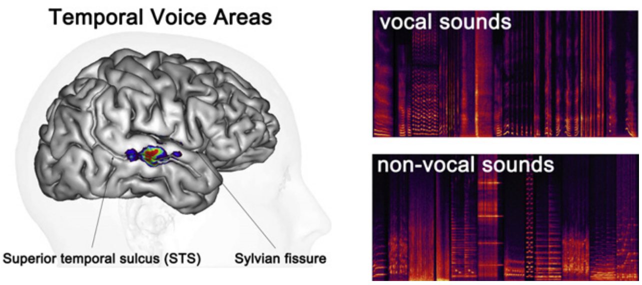

Figure 1. Temporal Voice Areas in the Adult Brain
The contrast of cerebral activity measured in the adult brain by functional magnetic resonance imaging (fMRI) in response to auditory stimulation with vocal versus non-vocal sounds (stimuli available at http://vnl.psy.gla.ac.uk) highlights voice selective TVA with greater activity in response to the vocal sounds. The TVA (shown here in an individual young adult subject) are mostly located along the middle and anterior parts of the superior temporal sulcus (STS) bilaterally.

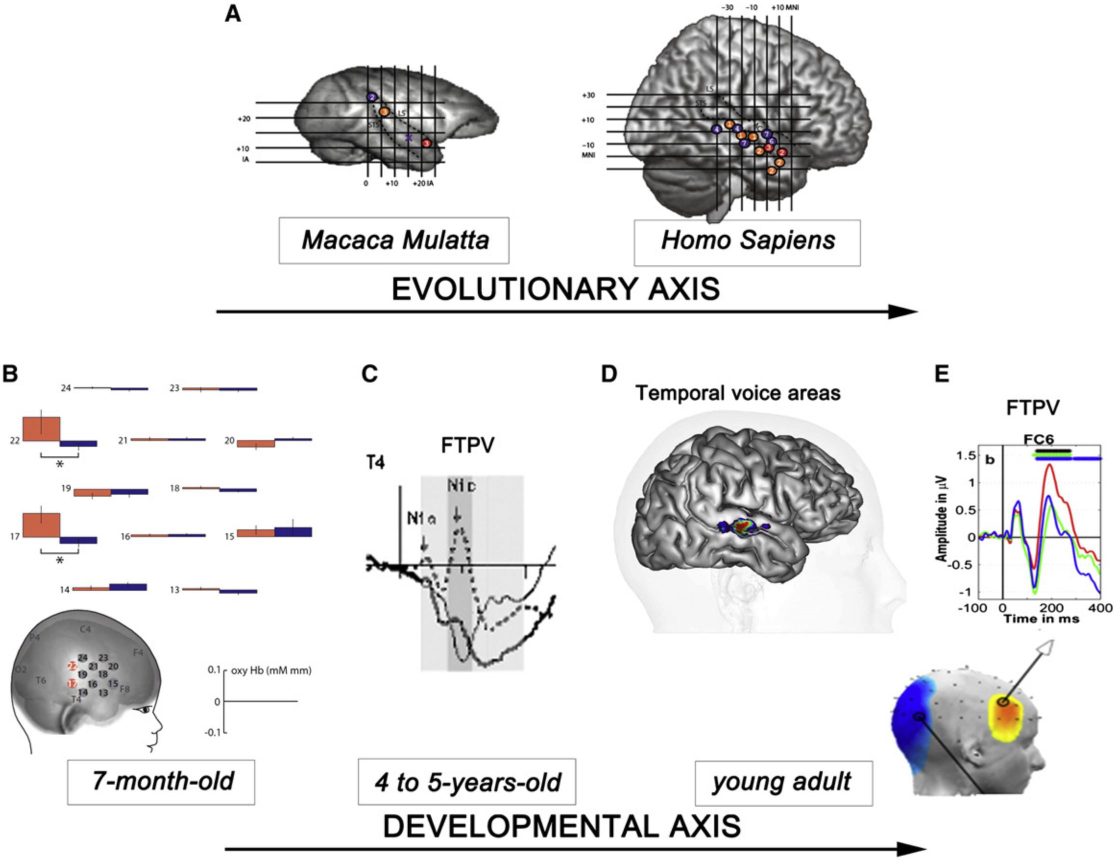

Figure 2. Phylogeny and Ontogeny of Cerebral Voice Processing

(A) Meta-analysis of neuroimaging studies of voice processing in monkeys and humans. Orange and purple circles: voice-selective regions showing greater activity in response to species-specific vocalizations compared to control sounds. Red circles: regions sensitive to speaker identity. Adapted from Petkov et al. (2009).

(B) NIRS study of cerebral response to vocal (orange) and nonvocal (blue) sounds in 7-month-old infants highlights bilateral regions of preferential response to voices in posterior temporal lobe, with greater voice sensitivity in the right hemisphere. No such response is observed in 4-month-old infants. Reproduced from Grossman et al. (2010).

(C) Auditory evoked potentials in 4- to 5-year-old children comparing vocal (bold line) to nonvocal (dashed line) sounds reveal a "fronto-temporal sensitivity to voice" (FTPV; light line = vocal-nonvocal) at electrode T4, peaking around 200 ms after sound onset, mostly apparent in the right hemisphere. y axis: AEP amplitude (μV). Positivities are downward. Reproduced from Rogier et al. (2010).

(D) Temporal voice areas in a young adult subject (cf. Figure 1).

(E) The FTPV observed in young adult subjects when comparing vocal sounds (red) to birdsongs (green) and environmental sounds (green), peaking at a latency of around 200 ms. Reproduced from Charest et al. (2009).

responses to voices versus other sounds in the posterior part of the temporal lobe bilaterally, with greater voice-sensitive response in the right hemisphere, while no brain region was found exhibiting the opposite pattern. In the 4-month-old infants, however, no such voice-sensitive response was observed.

A second experiment then examined the effects of affective information. Measures of blood oxygenation were acquired in 7-month-old infants during stimulation with affectively neutral sentences and sentences spoken with happy or angry emotional prosody. Two regions showed a significant modulation of their activity by affective content, both located in the right hemisphere: a region of posterior temporal cortex shown to be voice sensitive in experiment 1 and a region of the inferior prefrontal cortex, showing small responses but significantly greater for happy vocalizations.

These results provide the first available evidence of cerebral voice sensitivity in 7-month-old infants. Cerebral voice processing thus not only has a long evolutionary history (Petkov et al., 2008, 2009), it also develops relatively early in infants (Figure 2), long before speech perception is fully developed (Friederici, 2005). The pattern of voice sensitivity observed in infants by Grossmann et al. (2010) is comparable to the one observed in adult subjects. Yet the location of voice-sensitive cortex in infants appears more posterior than the one observed in adult (typically along middle/anterior STS, although the posterior temporal lobe posterior also exhibits significant voice sensitivity), suggesting that more anterior regions are not yet voice-sensitive 7 months after birth.

Second, they provide a precise timeline for the emergence of cerebral voice processing in infants. Measures of cerebral activity in 4-month-old infants do not show any evidence of regions responding more to sounds of voice compared to nonvocal sounds; in fact, they even showed the reverse pattern in one region, a rare occurrence in the adult brain. Only 3 months later, cerebral voice sensitivity has emerged. This highlights the period between 4 and 7 months after birth as critical for the development of cerebral voice processing.

Third, the findings highlight the crucial importance of the right hemisphere in the development of vocal communication in infants. The difference in voice sensitivity in the 7-month-old infants was much greater in the right than in the left hemisphere, as was the modulation by affective content. This indicates a central role of the "minor" right hemisphere, too often neglected, in the emergence of vocal communication ability in human infants.

Key Questions

Selectivity or Sensitivity?

In adults, the TVA are not only sensitive to voices, but also highly selective: they respond more to voice stimuli than to a range of control sounds, including acoustically matched control sounds, showing that the TVA's preference for voice stimuli is not simply driven by low-level acoustical parameters (Belin et al., 2000). Grossmann et al. (2010) demonstrate clear voice sensitivity in the 7-month-old brain; however, it is possible that this activity reflects the processing of low-level features more present in vocal sounds rather than voice processing per se. This is particularly the case for experiment 2, in which the greater response to affective (happy and angry) compared to neutral voices could reflect the processing of the many acoustical differences between these sound categories (e.g., f0 range) without implying emotional processing. Thus, it is important that follow-up experiments test the influence of acoustical structure by using additional control sound categories.

Anatomical and Behavioral Correlates?

During the first months after birth, synaptic proliferation continues at a high rate, associated with an exponential increase in metabolic activity during the first postnatal months (Chugani and Phelps, 1986). Myelination is also taking place at the same time. The auditory radiation that innervates Heschl's gyrus (containing the primary auditory cortex) shows apparent myelination at around 6 months of age (Nakagawa et al., 1998). Thus, between 4 and 7 months, the region of the temporal lobe where the TVA are located in adults is undergoing rapid structural changes, which may underlie the acquisition of specialization for voice processing. The precise time course of those structural changes in the STS still needs to be investigated more precisely. In parallel, behavioral studies of voice perception ability in this first year of life—not just speech perception, increasingly well understood (Friederici, 2005), but also, more relevant for infants, nonverbal voice perception—are required to fully understand how functional changes observed by Grossmann et al. (2010) translate at the behavioral level.

A Marker of Normal Cerebral Voice Development?

The fact that adults with autism sometimes show abnormal activation of the TVA (Gervais et al., 2004) suggests that children with disorders affecting vocal communication, such as autism, could also be characterized by anomalies of cerebral voice processing, that—one may speculate—could potentially be observable at an early stage of development. Grossmann et al. (2010) present results averaged across a group of 16 to 18 infants; whether or not NIRS can provide robust results at the individual level remains unclear. Nevertheless, the present findings open the important and exciting possibility of tools for assessing cerebral voice processing in infants and contributing to the early diagnosis and treatment of voice communication impairments in children.

REFERENCES

Belin, P., Zatorre, R.J., Lafaille, P., Ahad, P., and Pike, B. (2000). Nature *403*, 309–312.

Charest, I., Pernet, C.R., Rousselet, G.A., Quiñones, I., Latinus, M., Fillion-Bilodeau, S., Chartrand, J.-P., and Belin, P. (2009). BMC Neurosci. *10*, 127.

Chugani, H.T., and Phelps, M.E. (1986). Science *231*, 840–843.

Ethofer, T., Van De Ville, D., Scherer, K., and Vuilleumier, P. (2009). Curr. Biol. *19*, 1028–1033.

Friederici, A.D. (2005). Trends Cogn. Sci. *9*, 481–488.

Gervais, H., Belin, P., Boddaert, N., Leboyer, M., Coez, A., Sfaello, I., Barthélémy, C., Brunelle, F., Samson, Y., and Zilbovicius, M. (2004). Nat. Neurosci. *7*, 801–802.

Grandjean, D., Sander, D., Pourtois, G., Schwartz, S., Seghier, M.L., Scherer, K.R., and Vuilleumier, P. (2005). Nat. Neurosci. *8*, 145–146.

Grossmann, T., Oberecker, R., Koch, S.P., and Friederici, A.D. (2010). Neuron *65*, this issue, 852–858.

Kisilevsky, B.S., Hains, S.M., Lee, K., Xie, X., Huang, H., Ye, H.H., Zhang, K., and Wang, Z. (2003). Psychol. Sci. *14*, 220–224.

Nakagawa, H., Iwasaki, S., Kichikawa, K., Fukusumi, A., Taoka, T., Ohishi, H., and Uchida, H. (1998). AJNR Am. J. Neuroradiol. *19*, 1129–1136.

Ockleford, E.M., Vince, M.A., Layton, C., and Reader, M.R. (1988). Early Hum. Dev. *18*, 27–36.

Petkov, C.I., Kayser, C., Steudel, T., Whittingstall, K., Augath, M., and Logothetis, N.K. (2008). Nat. Neurosci. *11*, 367–374.

Petkov, C.I., Logothetis, N.K., and Obleser, J. (2009). Neuroscientist *15*, 419–429.

Rogier, O., Roux, S., Belin, P., Bonnet-Brilhault, F., and Bruneau, N. (2010). Int. J. Psychophysiol. *75*, 44–47.

Von Kriegstein, K., and Giraud, A.L. (2004). Neuroimage *22*, 948–955.