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Determinants of dominance: Is language laterality explained by physical or linguistic features of speech?

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The nature of cerebral asymmetry of the language function is still not fully understood. Two main views are that laterality is best explained (1) by left cortical specialization for the processing of spectrally rich and rapidly changing sounds, and (2) by a predisposition of one hemisphere to develop a module for phonemes. We tested both of these views by investigating magnetic brain responses to the same brief acoustic stimulus, placed in contexts where it was perceived either as a noise burst with no resemblance of speech, or as a native language sound being part of a meaningless pseudoword. In further experiments, the same acoustic element was placed in the context of words. We found reliable left hemispheric dominance only when the sound was placed in word context. These results, obtained in a passive odd-ball paradigm, suggest that neither physical properties nor phoneme status of a sound are sufficient for laterality. In order to elicit left lateralized cortical activation in normal right-handed individuals, a rapidly changing spectrally rich sound with phoneme status needs to be placed in the context of frequently encountered larger language elements, such as words. This demonstrates that language laterality is bound to the processing of sounds as units of frequently occurring meaningful items and can thus be linked to the processes of learning and memory trace formation for such items rather than to their physical or phonological properties.

Keywords: Speech; Sound; Word; Language; Auditory; Cortex; Hemisphere; Perception; Asymmetry (lateralization, laterality); Event-related (ERP, ERF); Magnetoencephalography; Mismatch negativity (MMN, mismatch field, MMF, MMNm); Human

Introduction

Since its first description in the late 19th century (Broca, 1861; Wernicke, 1874), language laterality in the human brain has never been fully understood. Right-handed individuals, whose first-order relatives are also right-handers, have an overwhelmingly high probability of having their language circuits lateralized to the left hemisphere (Hugdahl, 2000; Josse and Tzourio-Mazoyer, 2004). This means that a stroke to their left "dominant" hemisphere will likely leave them with a neurological language deficit or aphasia whereas a lesion in the right hemisphere will in most cases not be associated with a language deficit (Dronkers et al., 2004). Also, the brain is activated more strongly on the left side than on the right one when right-handed subjects engage in language tasks (Price, 2001; Tervaniemi and Hugdahl, 2003), and even when they are exposed to language they do not attend to (Pulvermüller et al., 2004; Shtyrov et al., 2003).

One main theory, which we here call the acoustic laterality theory, postulates that the physical properties of speech sounds are essential factors determining laterality to the left. Language sounds are spectrally rich and occupy a wide band of frequencies between a few hundreds and some thousands of hertz. In addition, some language sounds change rapidly over time. Stop consonants (such as [t], [p], or [k]), for example, can be realized as a brief plosion occurring after a silent period of defined length at the end of syllables. In this view, rapidly changing sounds are preferentially processed by the left dominant hemisphere, whereas tonal patterns that change slowly activate the right hemisphere more strongly than the left one (Fitch et al., 1997; Tallal et al., 1993; Zatorre and Belin, 2001; Zatorre et al., 2002). This acoustic theory explains a range of behavioral data according to which the right ear predominantly connected to the left hemisphere has an advantage in perceiving sounds with rapid changes. Such evidence comes from dichotic listening studies showing the so-called right ear advantage (REA) for CV syllables, plosive stop consonants, and even non-speech sounds with rapid transitions and high-frequency components, whereas vowels, fricatives, and slow acoustic transitions demonstrated a reduced or abolished REA (Deutsch, 1974; Fitch et al., 1993; Halperin et al., 1973; Schwartz and Tallal, 1980; Shankweiler and Studdert-Kennedy, 1967; Spellacy and Blumstein, 1970; Studdert-Kennedy and Shankweiler, 1970; Weiss and House, 1973). The idea of laterality for rapidly changing sounds also finds support in brain imaging studies (Belin et al., 1998; Celsis et al., 1999a,b; Fiez et al., 1995; Jaramillo et al., 2001; Johnsrude et al., 1997). However, this explanation on the basis of physical features

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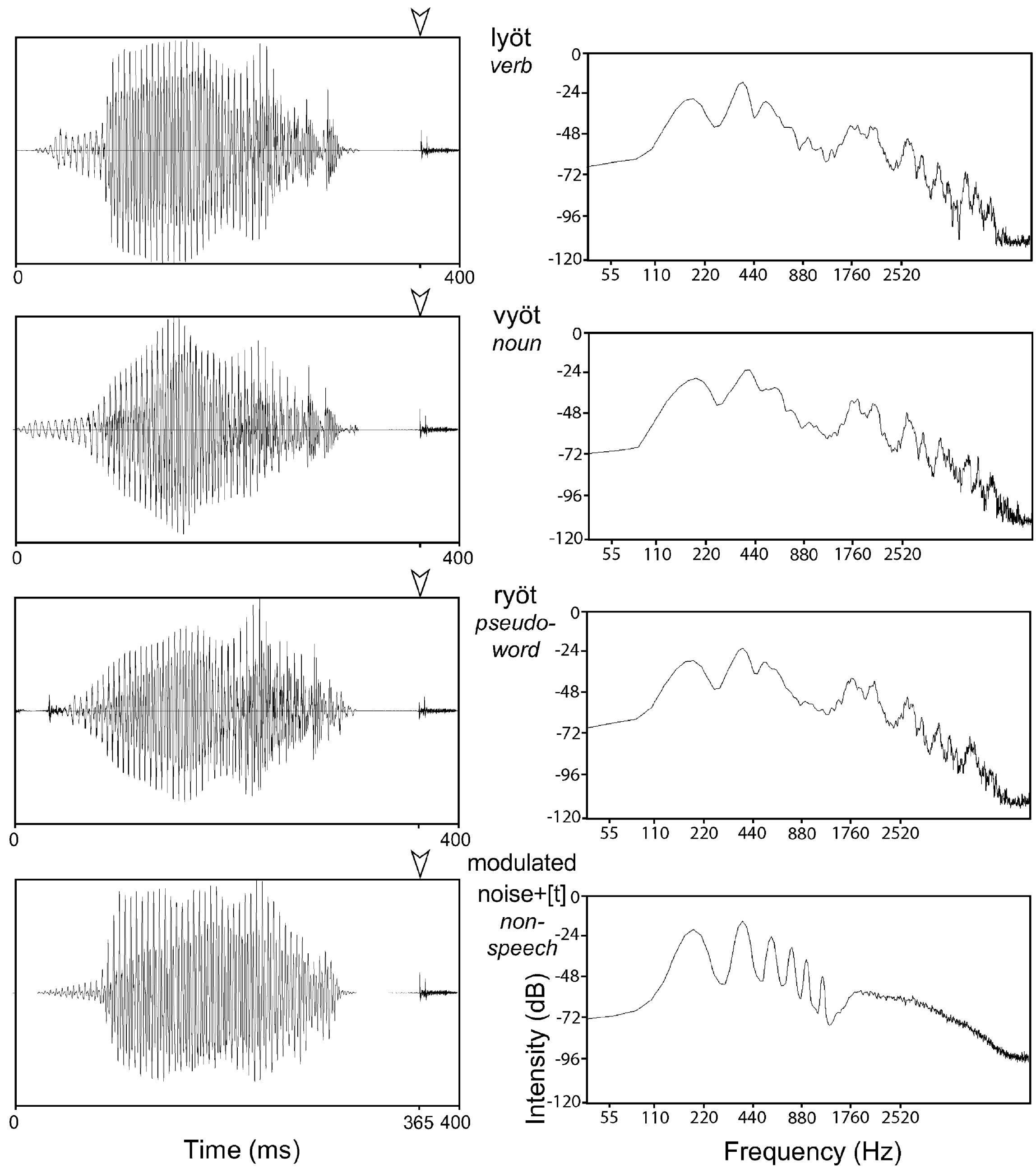

Fig. 1. The waveforms (left) and frequency component (FFT) analysis (right) of deviant acoustic stimuli used in the four experimental conditions: verb, noun, pseudoword, and non-speech complex sound. All stimuli were maximally matched for their acoustic properties. The standard and deviant stimuli in each condition are identical up to the divergence point at their end when the onset of final [t] takes place (marked with white arrowheads) in the deviant stimuli. This standard-deviant contrast is identical in all conditions, whereas the context in which it is presented varies (cf. Table 1).

has its limitations, because there are rapidly changing acoustic patterns that are not native speech sounds and that fail to elicit significantly lateralized responses (Best and Avery, 1999; Shtyrov et al., 2000b) and, vice versa, there are acoustically simple communication signals that do produce laterality (Gandour et al., 2000, 2003; Hsieh et al., 2000; Kujala et al., 2003; Papcun et al., 1974).

A major competing view, which we here call the phonological laterality theory, claims that non-speech and speech sounds are processed independently of each other and that there exists a specialized speech-processing module in the cortex. More specifically, it is argued that articulatory gestures are stored in the cortex and that their memory traces, which are thought to link sounds to corresponding articulation patterns, are preferentially treated by a putative dedicated speech module (e.g., Liberman and Whalen, 2000; Whalen and Liberman, 1987). If such a specialized mechanism indeed exists, it should be found in the perisylvian cortex of the left hemisphere (Braitenberg and Pulvermüller, 1992; Pulvermüller, 1999). This theory explains a number of psychoacoustic and psycholinguistic phenomena, among which the following is of interest here: short acoustic bursts perceived as stop consonants (e.g., [t]) when being a part of a spoken syllable, lose any resemblance with speech if presented in isolation or in conjunction with non-language sound (Liberman and Mattingly, 1988). This approach does provide a framework for explaining the