Brain & Language xxx (2013) xxx–xxx

Contents lists available at ScienceDirect

Brain & Language

journal homepage: www.elsevier.com/locate/b&l

Ventral and dorsal pathways of speech perception: An intracerebral ERP study

Agnès Trébuchon [a,b,c,*], Jean-François Démonet [d], Patrick Chauvel [a,b,c], Catherine Liégeois-Chauvel [a,b]

[a] INS INSERM, UMR 1106, 13005 Marseille, France
[b] Aix Marseille Université, 13000 Marseille, France
[c] Assistance Publique-Hôpitaux Marseille, 13005 Marseille, France
[d] Leenaards Memory Center, Departement Neurosciences Cliniques, CHUV, Rue du Bugnon 46, CH-1011 Lausanne, Switzerland

ARTICLE INFO

Article history:
Available online xxxx

Keywords:
ERP
Intracranial recordings
Speech perception
Ventral stream
Dorsal stream

ABSTRACT

Recent theory of physiology of language suggests a dual stream dorsal/ventral organization of speech perception. Using intra-cerebral Event-related potentials (ERPs) during pre-surgical assessment of twelve drug-resistant epileptic patients, we aimed to single out electrophysiological patterns during both lexical–semantic and phonological monitoring tasks involving ventral and dorsal regions respectively. Phonological information processing predominantly occurred in the left supra-marginal gyrus (dorsal stream) and lexico-semantic information occurred in anterior/middle temporal and fusiform gyri (ventral stream). Similar latencies were identified in response to phonological and lexico-semantic tasks, suggesting parallel processing. Typical ERP components were strongly left lateralized since no evoked responses were recorded in homologous right structures. Finally, ERP patterns suggested the inferior frontal gyrus as the likely final common pathway of both dorsal and ventral streams. These results brought out detailed evidence of the spatial–temporal information processing in the dual pathways involved in speech perception.

1. Introduction

Understanding the large-scale neural bases of speech processing remains a major quest in neuroscience. Apart from the classical temporal Wernicke's area and frontal Broca's area, neuroimaging studies have shown that language processing involves widespread brain regions, particularly within the temporal lobe, such as the superior temporal gyrus (STG), superior temporal sulcus (STS), middle temporal gyrus (MTG), and a postero-inferior area of the inferior temporal gyrus (ITG) (for review, see Price, 2012).

Current theories suggest that language is organized in widespread, segregated and overlapping networks (Mesulam, 1990). More recently a theory of a dual-stream processing in auditory language system, as described in visual modality has been proposed: the dorsal stream being involved in mapping speech sound to articulation, while the ventral one would support speech to meaning correspondences (Demonet, Thierry, & Cardebat, 2005; Hickok & Poeppel, 2007; Saur et al., 2008). From the superior temporal gyrus, which is engaged in early stages of speech perception, the system diverges into two processing streams. The dorsal stream, or "auditory–motor integration" pathway, runs dorso-caudally through the inferior parietal region and thence to premotor and prefrontal areas, especially so-called Broca's area. The "what" pathway for speech or ventral stream projects ventro-rostrally to the anterior part of the middle and inferior temporal gyri and serves as a sound-to-meaning interface by mapping sound-based representations of speech to widely distributed conceptual representations.

Early neuroimaging PET studies (for a review Price, 2012) identified distinct neural systems involved with phonology and lexical–semantic processing. Demonet et al. (1992, 1994) used a dual paradigm comprising a phonological task during which the subject had to monitor the sequential phonemic organization of pseudo-words and a lexico-semantic task during which the subject monitored concrete adjectives and object names. Whereas phonological processing involved perisylvian areas, lexico-semantic processing was particularly associated with activity in the left middle and inferior temporal gyri, in addition to the superior temporal regions.

A large body of neuroimaging data subsequently confirmed this dichotomy between the two main levels of speech processing, namely segmented phonology and lexical semantics, without directly addressing the question of the dorsal/ventral dual stream organization.

Recently, based on the idea of large-scale networks comprising specialized brain areas (network nodes) and their interconnecting

* Corresponding author at: INS INSERM, UMR 1106, Faculté de Medecine Timone, Aix Marseille Université, 13005 Marseille, France.
E-mail address: agnes.trebuchon@univ-amu.fr (A. Trébuchon).

0093-934X/$ - see front matter © 2013 Elsevier Inc. All rights reserved.
http://dx.doi.org/10.1016/j.bandl.2013.04.007

white matter fiber tracts (network connections), Saur et al. combined fMRI with a diffusion tensor imaging (DTI) to test the neuroanatomical basis of the "dual-stream model" of language (Saur et al., 2008). This work neatly revealed that a sublexical, phonological speech task (pseudoword repetition) was sustained by a dorsal pathway, connecting the superior temporal lobe and premotor cortices in the frontal lobe via superior longitudinal fascicle and its arcuate sub-component. By contrast, higher-level language comprehension task was mediated by a ventral pathway connecting the middle temporal lobe and the ventrolateral prefrontal cortex via the extreme capsule.

Measuring event-related potentials has been fundamental in understanding the temporal dynamics of language processing. The findings from a number of studies have shown that all words and meaningful items elicited a negative-going voltage deflection peaking around 400 ms after stimulus onset (N400) (Kutas & Federmeier, 2000; Kutas & Hillyard, 1984 for a review). Although there have been a number of interpretations of the functional significance of the N400, it is most widely considered to be an index of lexical and semantic processing (for a review see Lau, Phillips, & Poeppel, 2008). Most studies addressing the neural bases of semantic processing pinpoint the involvement of the ventral stream. Magnetoencephalography (MEG) studies brought up evidence of the left mid-posterior temporal cortex as one of the major sources of the semantic relatedness N400 effect (Halgren et al., 2002). Using anatomically constrained MEG, Marinkovic et al., investigated the spatio-temporal characteristics of word comprehension during a semantic judgment task and described the dynamics of the underlying neural processing in the ventral stream (Marinkovic et al., 2003). Recorded activity spread from the primary auditory cortex (55 ms after the stimulus onset) to bilateral anterior temporal and inferior prefrontal regions around 400 ms. Few works have focused specifically on the spatio-temporal distribution of neural activities supporting phonological processing. Tracking cortical processing of spoken words and pseudo-words, Helenius, Parviainen, Paetau, and Salmelin (2009) showed that speech stimuli evoked a transient peak at 100 ms (N100m) followed by a longer-lasting activation peaking at around 400 ms (N400m) in the left and right temporal cortex (Helenius et al., 2009). The authors assumed that there is a parallel activation of phonological–lexical and semantic representations reflected in the onset phase of the N400m activation, starting around 200 ms with culmination around 400 ms in the case of lexical selection while a sustained response continues further on for pseudo-word condition. Based on these studies, it is difficult to differentiate phonological from lexical processes since ERP differences between words and pseudo-words are observed only in late latencies. However, a negativity arising earlier than N400 (around 300 ms) has been described as being specifically linked to phonological processes and called the phonological mapping negativity (PMN) (Connolly and Phillips, 1994; Connolly, Stewart, & Phillips, 1990; Thierry, Doyon, & Demonet, 1998). This component recorded in response to words as well as pseudo-words was not modulated by the lexical factor, contrary to the N400, but appeared to be sensitive to phonological expectation rather than lexical expectation. It was found to be localized over parietal electrodes (Newman & Connolly, 2009).

The main goal of the present study was to characterize the time course of neural activities during word and pseudo-word processing respectively, using brain-implanted electrodes so that neural activities in structures involved in either the ventral or the dorsal stream; phonological processing was expected to elicit specific ERP changes in structures belonging to the dorsal pathway while semantic processing would have distinctive counterparts in ERPs recorded in the ventral structures.

To achieve simultaneous high spatial and temporal resolution, we recorded evoked potentials to both words and pseudo-words from many different brain regions in a group of patients with drug-refractory epilepsy in whom 6–10 depth electrodes were implanted in pre-surgical evaluation procedures.

2. Materials and methods

2.1. Patients

Twelve patients (8 women, 4 men), aged 16–55 (mean 31 years) who had drug-refractory epilepsy and were undergoing evaluation of possible surgical intervention were studied. Stereoelectroencephalographic (SEEG) recording was performed in order to define the epileptogenic zone (Bancaud & Talairach, 1973). The choice of electrode location was based on pre-SEEG clinical and video-EEG recordings and made independently of the present study. This study did not add any invasive procedure to depth EEG recordings. Seventy to 128 intracerebral contacts were simultaneously recorded in each patient. This study was approved by the institutional Review Board of the French Institute of Health (IRB0000388, FWA00005831). All patients signed informed consent prior to participation. .

Event related potential (ERP) recordings were part of the functional mapping procedure (language, memory, and/or vision, depending on each case of epilepsy) carried out in each subject. Anticonvulsant therapy was reduced or withdrawn during the SEEG exploration in order to facilitate seizures. However, no subject had seizures in the 12 h before ERP recordings. Electrodes with slow waves or epileptic spikes were not included in this analysis.

A standard Oldfield test indicated that 10 patients were right-handed, and 2 patients left-handed (Oldfield, 1971). Language-dominance was assessed by functional MRI and ictal/postictal speech disturbance, and when doubt persisted, a Wada test was performed (P11). Ten patients had left-hemisphere specialization for language and 2 patients (P11, P12) had atypical language representation (right-hemisphere specialization). The demographic and clinical data as well as localization of epilepsy and recorded structures are summarized in Table 1.

2.2. Stimuli and Tasks

There were two tasks adapted from Demonet and colleagues (Demonet et al., 1992; Thierry et al., 1998). The paradigm involved a phoneme task performed on pairs of pseudo-words and a lexical semantic task on adjective–noun pairs. In the present study we focused on evoked responses to the first non-target item either pseudo-words or adjectives avoiding the effect of attention.

In the phoneme task, the non-word was a consonant-vowel bisyllabic letter string checked for meaningless features in French (e.g. catu, siju, roda ...). Patients had to identify a /b/ in a second pseudo-word when preceded by a /d/ in a first pseudo-word (e.g. ro/d/a fo/b/u) by pressing a designated button with the right hand (HOLD condition). In response to every other stimuli couple not fulfilling these criteria, the patient was required to press the other button with the same hand (RELEASE Condition). The phoneme /d/, if present, was always set in the second syllable of the first pseudo-word. Fifty percent of the stimuli were lacking a /d/ in the first pseudo-word (RELEASE condition) and might or might not contain a /b/ in the second pseudo-word. The consonant distracters for /d/ and /b/ were /t/ and /p/, respectively, in 50% of the cases.

In the word task, the same sequential structure was used and stimuli were also twofold while consisting of adjective–noun pairs. The task was to identify animal names denoting animals smaller than a rabbit when preceded by an adjective with a positive meaning, for example, "beau canari" ("nice canary") (HOLD condition). Six adjectives sharing 'positive' meaning (e.g., nice, sweet) and

Please cite this article in press as: Trébuchon, A., et al. Ventral and dorsal pathways of speech perception: An intracerebral ERP study. *Brain & Language* (2013), http://dx.doi.org/10.1016/j.bandl.2013.04.007