Available online at www.sciencedirect.com

ScienceDirect

BioSystems 89 (2007) 198–207

BioSystems

www.elsevier.com/locate/biosystems

Functional connections between auditory cortical fields in humans revealed by Granger causality analysis of intra-cranial evoked potentials to sounds: Comparison of two methods

Hiroyuki Oya[a,1], Paul W.F. Poon[a,b,*], John F. Brugge[a,2], Richard A. Reale[a,3], Hiroto Kawasaki[a,4], Igor O. Volkov[a,5], Matthew A. Howard III[a,6]

[a] *Department of Neurosurgery, University of Iowa College of Medicine, Iowa City, IA 52242, USA*

[b] *Department of Physiology, National Cheng Kung University, College of Medicine, Tainan, Taiwan*

Received 16 December 2005; accepted 20 May 2006

Abstract

Knowledge of neural interactions amongst cortical sites is important for understanding higher brain function. We studied such interactions using Granger causality (GC) to analyze auditory event-related potentials (ERPs) recorded directly and simultaneously from two physiologically identified and functionally interconnected auditory areas of cerebral cortex in human neurosurgical patients. Two methods of GC analysis were used and the results compared. Both approaches involved adaptive autoregressive modeling but differed from each other in other ways. Results obtained by using the two methods also differed. Fewer false-positive results were obtained using the method that suppressed the ERP non-stationarity and that expressed the GC as the sum of model coefficients, which suggests that this is the more appropriate approach for analyzing ERPs recorded directly from the human cortex.

Keywords: Granger causality; Auditory cortex; Cortical connectivity; Intracranial recording; Vocal sound; Autoregressive modeling

1. Introduction

Auditory cortex of the human is located on the superior temporal gyrus of the temporal lobe. It is made up of multiple fields that are thought to be interconnected and organized into three hierarchical processing levels referred to as the auditory 'core', 'belt' and 'parabelt'. This organizational model, which was originally derived from anatomical and physiological studies in non-human primates, is seen operating in a hierarchical fashion to process complex acoustic signals, such as communication sound and speech (reviewed by Kaas and Hackett, 2000; Rauschecker, 1998). Although this model has been posited for human cortex (Binder et al., 2000; Wessinger et al., 2001), there has been little direct experimental evidence for the cortico-cortical connec-

* Corresponding author at: Department of Physiology, National Cheng Kung University, College of Medicine, Tainan, Taiwan. Tel.: +886 6 235 3535x5458; fax: +886 6 236 2780.

E-mail addresses: hiroyuki-oya@uiowa.edu (H. Oya), ppoon@mail.nkcu.edu.tw (P.W.F. Poon), john-brugge@uiowa.edu (J.F. Brugge), reale@physiology.wisc.edu (R.A. Reale), hiroto-kawasaki@uiowa.edu (H. Kawasaki), igor-volkov@uiowa.edu (I.O. Volkov), matthew-howard@uiowa.edu (M.A. Howard III).

[1] Tel.: +1 319 384 9846; fax: +1 319 353 8737.
[2] Tel.: +1 319 353 7082; fax: +1 319 353 8737.
[3] Tel: +1 608 263 5851; fax: +1 608 263 5929.
[4] Tel.: +1 319 384 8239; fax: +1 319 353 8737.
[5] Tel.: +1 319 335 8968; fax: +1 319 384 4830.
[6] Tel.: +1 319 356 8468; fax: +1 319 353 8737.

0303-2647/$ – see front matter © 2006 Elsevier Ireland Ltd. All rights reserved.
doi:10.1016/j.biosystems.2006.05.018

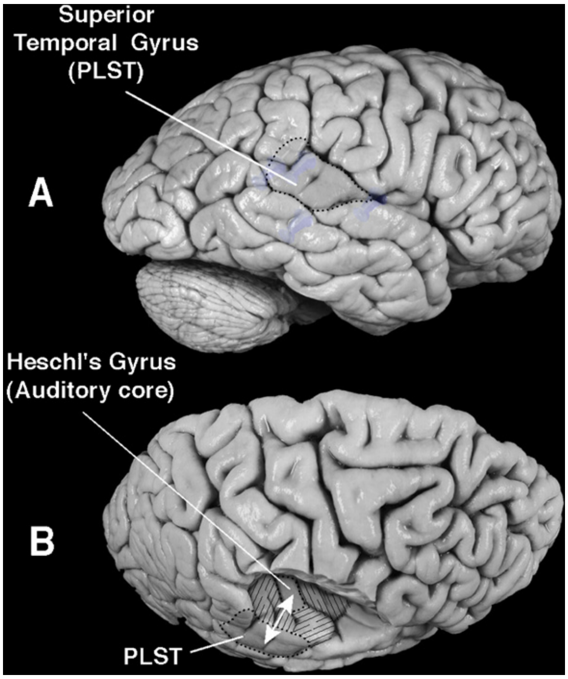

Fig. 1. Two views of human brain specimen showing the locations of the posteriolateral superior temporal field (PLST) on the superior temporal gyrus and the auditory core area on Heschl's gyrus (HG). (A) Lateral view of the surface of the right cerebral hemisphere showing PLST. (B) HG and surrounding cerebral cortex viewed from above after removing overlying parietal lobe. Arrows indicate the functional connectivity between HG and PLST.

tions required to support such a processing scheme. The anatomical tract-tracing methods that have been used so effectively in mapping auditory cortical fields and their connectivity in the living monkey brain cannot be used in humans. An alternative method of tracing auditory cortico-cortical pathways in the human brain involves focal electrical stimulation of one cortical site while systematically mapping the resultant evoked activity from distant sites (Brugge et al., 2003, 2005; Greenlee et al., 2004; Howard et al., 2000; Liegeois-Chauvel et al., 1991; Matsumoto et al., 2004). Using this approach we have shown functional connectivity between auditory cortex on mesial Heschl's gyrus (HG), which we consider to be core cortex, and an auditory area on the lateral surface of superior temporal gyrus, which we refer to as the posterior lateral superior temporal field (PLST) and interpret to be a part of the auditory belt or parabelt (Brugge et al., 2003, 2005; Howard et al., 2000). Fig. 1 shows on a human brain specimen the location of these two auditory fields, with arrows indicating the reciprocal functional connectivity between them.

Electrical mapping of functional connectivity patterns in temporal cortex provides important information on timing, topography and direction of neural transmission, but leaves open the question of functional interactions presumably taking place between the interconnected fields under normal listening conditions. One approach to gaining this information is the so-called Granger causality (GC, Granger, 1969; Freiwald et al., 1999). Granger causality is defined in statistical terms and expressed as predictability: one stochastic process is causal to another if at a given time point the predictability of the second process is improved by including measurements from the immediate past of the first. When applied to interactions between distant brain sites, knowledge about the activity recorded from one cortical location has been used to predict activity recorded simultaneously at a second location (Brovelli et al., 2004; Chen et al., 2004; Ding et al., 2000; Hesse et al., 2003; Kaminski et al., 2001; Liang et al., 2000).

In the present study we measured during passive listening in humans the directional interactions that occurred between the core auditory cortex on posteromesial HG and auditory cortex on posterior lateral superior temporal gyrus, areas which have been shown previously to be functionally interconnected (Brugge et al., 2003, 2005; Howard et al., 2000). Data were auditory event-related potentials (ERPs) recorded directly from the cortex of neurosurgical patients. ERPs belong to the class of non-stationary signals (Oppenheim and Schafer, 1975) in which both mean voltage and variance tend to vary over time. Time-variant approaches to estimate GC are required to account for this non-stationary property. Two time-variant GC methods have been employed in the past to study functional interactions in the brain. One (Method 1) analyzed ERPs recorded from the scalp (Hesse et al., 2003) while the second (Method 2) analyzed local field potentials recorded intra-cranially (Ding et al., 2000; Kaminski et al., 2001). Both methods involve an adaptive autoregressive model but differ from each other in two important respects. First, Method 2 but not Method 1 pre-processes data to suppress signal non-stationarity. As we will demonstrate, skipping the pre-processing step can result in spurious causality responses. Second, Method 1 uses a ratio of error-variance produced by bi-variant modeling, whereas Method 2 employs the sum of coefficients on the off-diagonal coefficient matrices. Although both methods can be considered causality measures in the Granger sense, taking a ratio and interpreting its results needs to be done with care. At the start of our work it was unclear to us which approach would best apply to our near-field ERPs, hence we carried out GC analyses on the same dataset using both approaches and compared the results obtained.