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The functional role of the frontal cortex in pre-attentive auditory change detection

Chun-Yu Tse [a], Teemu Rinne [b], Kwun Kei Ng [c], Trevor B. Penney [c,d,*]

[a] Temasek Laboratories, National University of Singapore, Singapore
[b] Institute of Behavioural Sciences, University of Helsinki, Finland
[c] Department of Psychology, National University of Singapore, Singapore
[d] LSI Neurobiology/Aging Programme, National University of Singapore, Singapore

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ABSTRACT

Accounts of the functional role of the frontal cortex in pre-attentive auditory change detection include attention switching, response inhibition, contrast enhancement, and activation of a predictive model. These accounts assume different sequential activation patterns between the temporal and frontal cortices: Change detection in the auditory areas of the superior temporal cortex (STC) followed by inferior frontal cortex (IFC) activation for attention switching and response inhibition; STC preceded by IFC activation for contrast enhancement; and an IFC–STC–IFC activation sequence for the predictive model. We used the event-related optical signal (EROS), which provides a temporal resolution of milliseconds and a spatial resolution of 5 to 10 mm, combined with lagged correlation path modeling to examine the response of the right frontal and temporal cortices to auditory duration deviants of varying magnitude. Event-related potentials (ERPs) were also recorded, as was the slow optical (hemodynamic) brain response. The data analyses revealed temporal–frontal, frontal–temporal–frontal, and temporal–frontal activation patterns when the deviants represented relatively large, medium, and small changes from the standard stimulus, respectively. These results indicate that the degree of deviance modulates spatio-temporal dynamics within the STC–IFC auditory change detection network.

Introduction

Violations of regularity in the auditory environment elicit a scalp-recorded event related potential (ERP) response even when the auditory channel is unattended (Näätänen and Michie, 1979; Näätänen et al., 2007). This automatic change detection response, termed the mismatch negativity (MMN), appears to be generated within the temporal and frontal cortices (see Deouell, 2007 for review), as indicated by results from ERP source localization (e.g., Giard et al., 1990), functional magnetic resonance imaging (fMRI; Doeller et al., 2003; Molholm et al., 2005; Opitz et al., 2002; Rinne et al., 2005), positron emission tomography (PET; Müller et al., 2002), and optical imaging (Rinne et al., 1999; Tse and Penney, 2007, 2008; Tse et al., 2006).

Although it is generally accepted that the auditory cortex represents auditory change detection, the functional role of the frontal cortex in MMN generation is still debated. An early view held that the frontal cortex underlies attention shifting (e.g., Escera et al., 2000; Giard et al., 1990; Näätänen, 1990; Rinne et al., 2000). When a change is detected, attention is reoriented for further stimulus processing and the probability of attention reorientation is higher, when the change is salient. However, data from fMRI studies of auditory change detection suggest that recruitment of the frontal cortex decreases with increasing deviance (Opitz et al., 2002; Rinne et al., 2005). Opitz et al. (2002) interpreted this data pattern as indicating that the frontal cortex enhances the contrast between the deviant and standard stimuli when the stimulus change is difficult to detect. However, Rinne et al. (2005) proposed that the frontal cortex inhibits down-stream attention or response mechanisms so that small deviations do not elicit further processing. Hence, the frontal cortex is more responsive to small than large changes because inhibition is required for the former, but not the latter. The regularity-violation hypothesis (Winkler, 2007), in turn, posits that a predictive model derived from previous auditory input is used for initial processing of subsequent auditory input. If the model fails to predict the properties of the auditory signal, the deviant is detected (i.e., a MMN is elicited), and the predictive model is updated. However, the regularity-violation hypothesis does not identify the brain structure(s) involved, although other research suggests that the frontal cortex may participate in the model updating process (Bledowski et al., 2004; Kirino et al., 2000; Knight, 1984; Polich, 2007).

These hypotheses, which postulate pre- and/or post-change detection processes in the frontal cortex, predict different sequential activation patterns between the frontal and temporal cortices. If the frontal cortex participates in a pre-change detection process (e.g., contrast

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[*] Corresponding author at: Department of Psychology, Faculty of Arts and Social Sciences, 9 Arts Link, National University of Singapore, 117570, Singapore. Fax: +65 6773 1843.

E-mail address: penney@nus.edu.sg (T.B. Penney).

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enhancement or predictive model generation/activation) it should be active before the temporal areas responsible for change detection. Grimm et al. (2011) demonstrated a deviance response in the middle latency range (MLR; within 50 ms of deviance onset), which may serve as the source initiating the contrast enhancement system or predictive model. However, if the frontal cortex activity is related to a post-change detection process (e.g., attention switching, response inhibition, predictive model updating), then temporal cortex activity should precede frontal cortex activity.

Here, we used non-invasive fast optical imaging (see Gratton and Fabiani, 2010) in combination with a lagged correlation path modeling method (Rykhlevskaia et al., 2008) to reveal the spatiotemporal dynamics of temporal and frontal cortex involvement in deviance detection. Although earlier studies that used other methods suggested functional connectivity between STC and IFC in pre-attentive change detection (i.e., phase synchronization of MEG data, (Hsiao et al., 2010); dynamic causal modeling of EEG data, (Garrido et al., 2009)), to our knowledge, the present study is unique in showing that functional connectivity in the STC–IFC auditory change detection network is modulated by deviance magnitude.

Material and methods

Participants

Thirty-two undergraduate students (16 females) ranging in age from 19 to 22 years old participated in the study. According to self-report, all participants had normal hearing, were not taking any psychoactive medications, and had no history of neurological disorders or head trauma. All participants met the Edinburgh Handedness Inventory (Oldfield, 1971) criterion for right handedness.

Stimuli and procedure

The stimuli were identical to those used by Rinne et al. (2005). Complex tones comprised 500 Hz, 1000 Hz, and 1500 Hz components with rise and fall times of 5 ms. The first and second harmonics were two and three times higher in frequency and 3 and 6 dB lower in intensity than the fundamental frequency.

In the experimental block, 88% of the stimuli were 75 ms standard tones. The remaining 12% were distributed among 35 ms, 25 ms, and 15 ms deviant tones (4% each) to create the Small, Medium, and Large deviant conditions, respectively. We used duration decrements as deviants because the decrease in stimulus energy should not enhance the amplitude of obligatory ERPs (e.g., N1), with the result that any activation enhancements to duration deviants can be directly associated with processing of the change. Furthermore, a relatively low deviant probability was used to ensure a prominent frontal effect (Sato et al., 2000). Sixty deviant tones (20 tones for each deviant condition) and 440 standard tones were presented at a comfortable hearing level of about 70 dB SPL in each of 12 experimental blocks conducted for each of the two EROS recording montages (i.e., light source/detector configurations; see Fig. 1). The onset-to-onset interval between adjacent tones was 500 ms and Montage B differed from Montage A by shifting the source/detector configuration one column anteriorly.

There were three control block types, each comprising one of the deviant tones from the experimental block (i.e., 35, 25 or 15 ms) only. These blocks permitted comparison of the brain responses elicited by the same physical stimulus when it served as a deviant and as a standard. There were 500 tones in each control block and the onset-to-onset interval was 500 ms. For each of the EROS recording montages, each control block type was run 4 times (12 blocks in total per montage). The experimental and control blocks were interleaved and the order of control blocks was counterbalanced across participants. Each participant watched a self-selected subtitled movie presented without sound. Participants were instructed to ignore the tones presented via headphones.

Event related potential recording and analysis

Event-related potentials (ERPs) were recorded from five scalp locations (Fz, Cz, Pz, A1, and A2 according to the 10–20 system). Three additional electrodes, two placed on the left and right outer canthi and one below the right eye, were used to record horizontal and vertical EOG. The reference electrode was placed on the nose and the ground electrode was placed at about the C4 position. The impedance of all electrodes was at or below 5 kΩ. The EEG was sampled at 256 Hz (REFA-64 amplifier, TMS International, The Netherlands) from DC to 70 Hz, and was filtered offline with a 0.1–20 Hz band pass filter. ERP waveforms, time-locked to tone onset and averaged in 300 ms epochs with a pre-stimulus baseline of 100 ms (EEProbe, ANT BV, Enschede, The Netherlands), were generated separately for each deviant and standard condition.

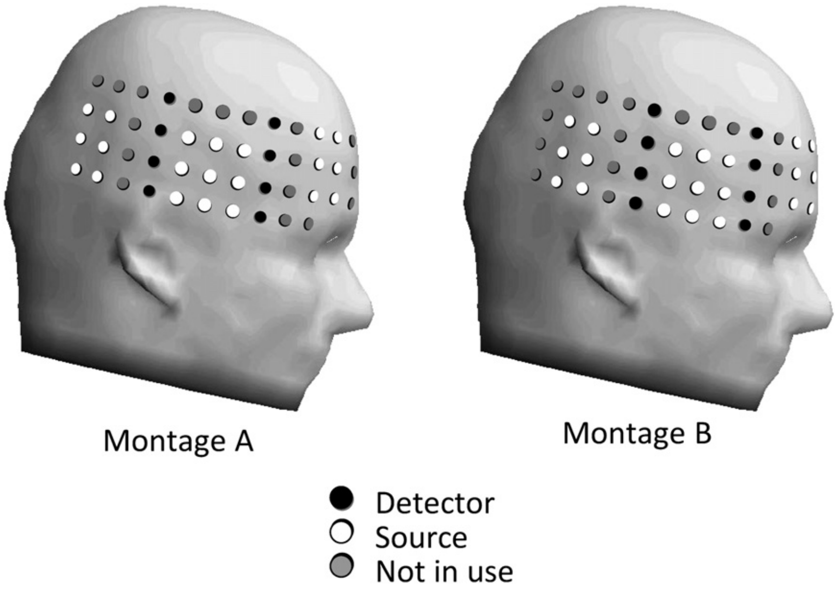

Fig. 1. Two recording montages were used to record optical data from a total of 240 source–detector pairs. Black and white circles represent the *locations* of source and detector fibers. Gray circles represent locations not in use on the recording montages.